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1910.

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# NEW GENERIC TERM

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PROCEEDINGS  
OF THE  
GENERAL MEETINGS FOR SCIENTIFIC BUSINESS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.  
(April to June, 1910.)

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April 5, 1910.

Prof. E. A. MINCHIN, M.A., Vice-President,  
in the Chair.

The Secretary exhibited a series of photographs taken in the South Orkneys in 1908 by a correspondent of 'The Times,' and kindly sent to him by the Editor of 'The Times.' The photographs included views of scenery and an interesting series of studies of living Seals, such as the Sei-Leopard (*Stenorhynchus leptonyx*), Weddell's Seal (*Leptonychotes weddellii*), the White, or Crab-eating Seal (*Lobodon carcinophagus*), and Ross's Seal (*Ommatophaga rossi*).

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Mr. R. I. Pocock, F.L.S., F.Z.S., exhibited a living specimen of a Mole-Rat (*Georychus*) recently presented to the Society by Capt. C. H. Armitage, who brought it from Ashanti. Mr. Pocock remarked that the animal possibly belonged to the species from Togoland described by Matschie as *G. zechi*, and certainly represented a form never previously exhibited in the Gardens.

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The following papers were read :—

1. The Caudal Fin of the TELEOSTOMI.  
By RICHARD H. WHITEHOUSE, M.Sc.,  
University of Birmingham.\*

[Received February 4, 1910.]

(Plates XLVII.—L.† and Text-figure 57.)

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1. Introduction, p. 590.
2. Terminology, p. 592.
3. Morphology, p. 593.
4. General Conclusions, p. 620.
5. Additional Note, p. 623.

1. INTRODUCTION.

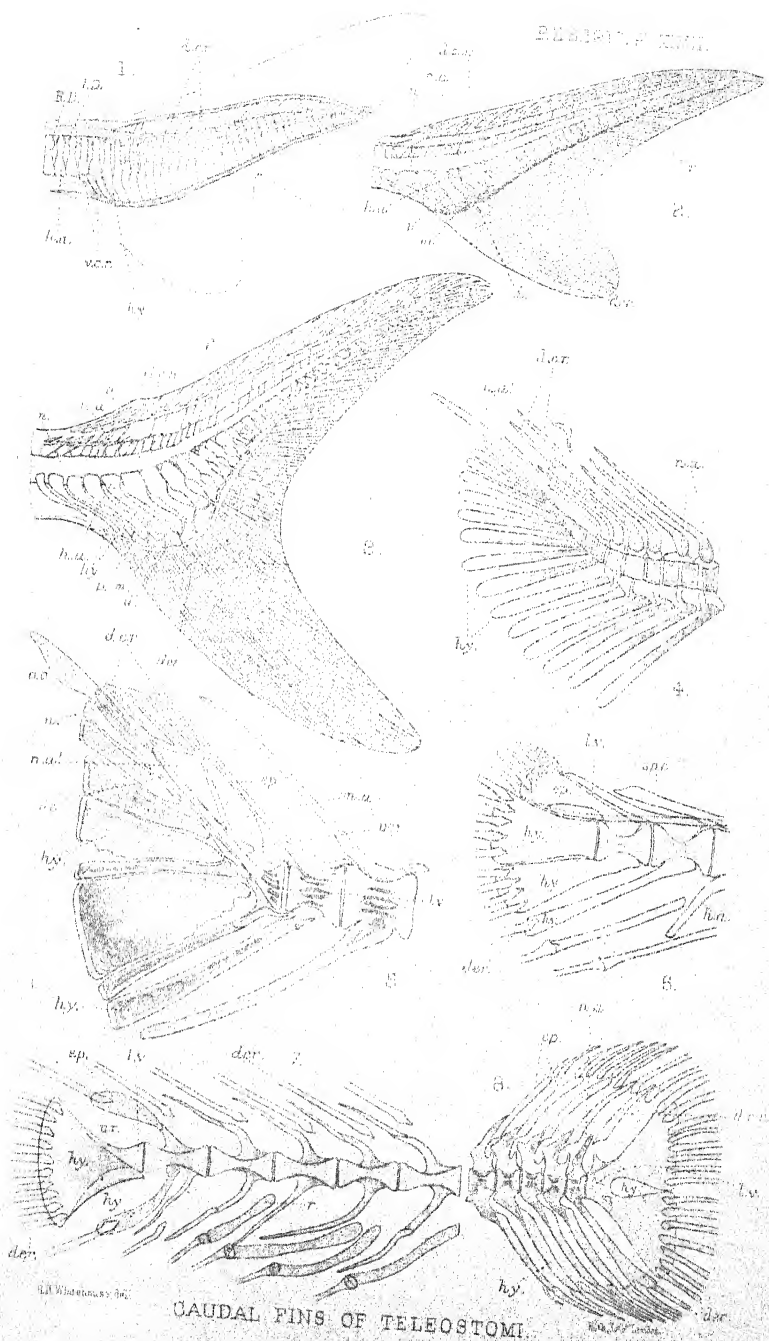
While the study of the paired fins of fishes, and also the dorsal and anal among the median unpaired fins, has been prosecuted in great detail, a systematic, detailed investigation of the caudal fin seems to have received much less attention. Some authors have dealt somewhat extensively with the subject, yet these have only treated of a comparatively few species; it was thought advisable, therefore, that such an important organ as the caudal fin of fishes should receive a broad treatment, and to carry out this purpose, several scores of different species have been subjected to a detailed examination of the skeletal parts of the fin. The number treated of includes species from as many widely different families as it has been possible to obtain, so that almost every form of tail likely to occur should be made known. It is impossible to include every type examined in the present paper, but the subject will be completed at as early a date as possible.

The Teleostei will receive the fullest treatment, but some reference will be made to other groups for the sake of presenting a more complete account of the piscine tail-fin. It has been impossible, as yet, to investigate the tail of the Dipnoi, but it is hoped that this group also will be dealt with in due course.

Material for the work has been obtained from various sources, the largest quantity having been obtained at Naples during my occupation of the British Association table at the Zoological Station in that town, during the six months ended May, 1908. Other valuable material has been supplied to me by a number of friends. I should like to mention here that the whole investigation is due to the suggestion of the late Professor Bridge, F.R.S., under whose superintendence the work was carried out; it was a pleasure and fortune to have so able a critic and kindly adviser as my late revered teacher. I wish also to express my best thanks to the British Association for appointing me to occupy their table

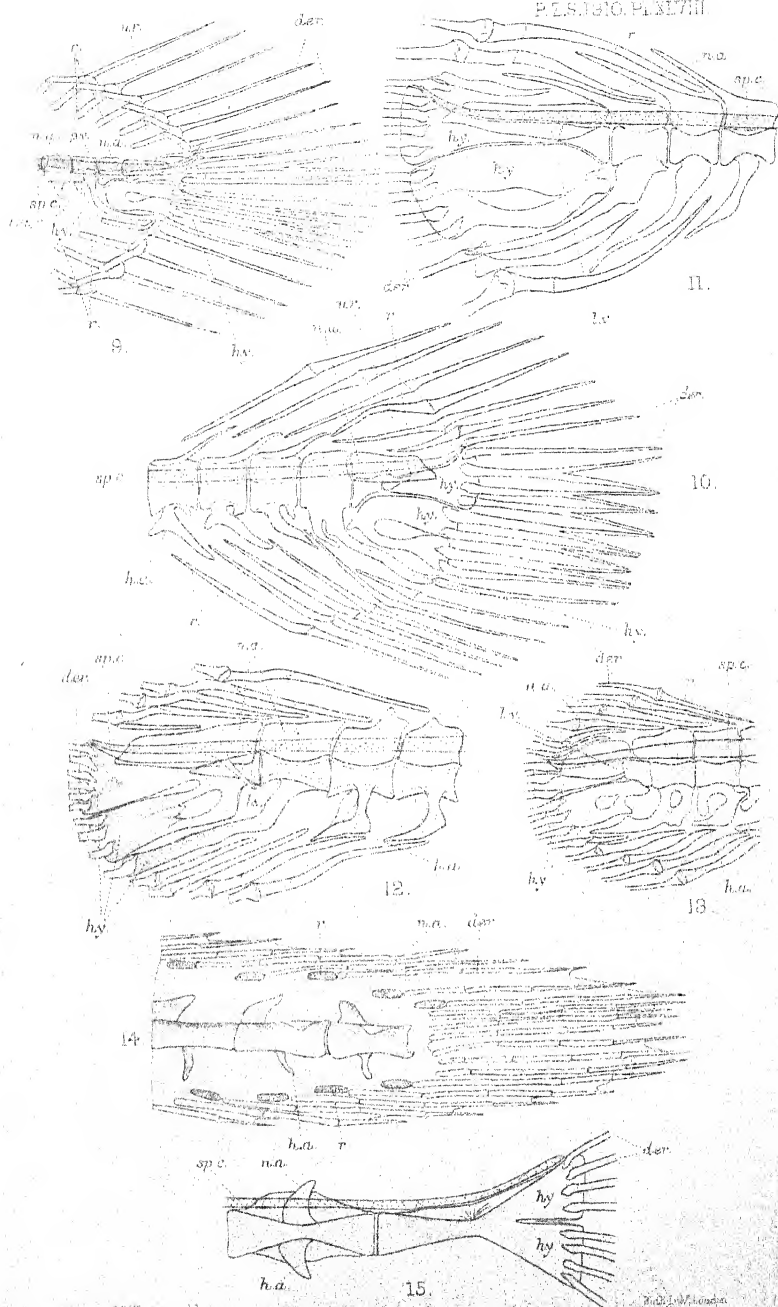
\* Communicated by Dr. P. CHALMERS MITCHELL, M.A., F.R.S.

† For explanation of the Plates see p. 625.



CAUDAL FINS OF TELEOSTOMI



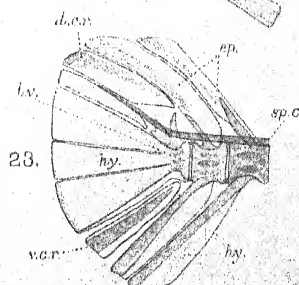
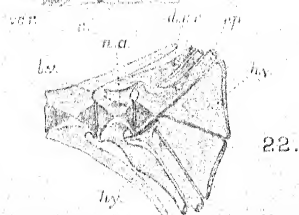
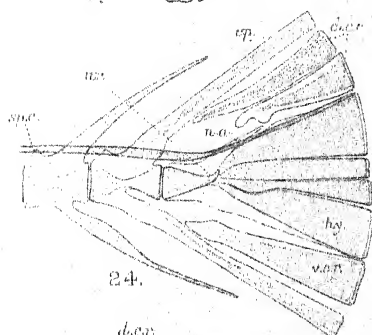
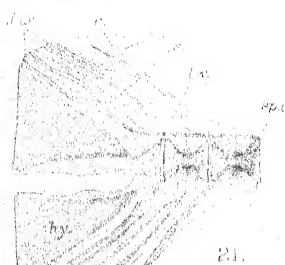
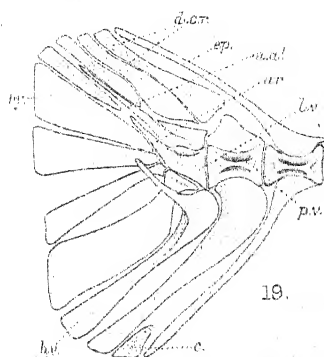
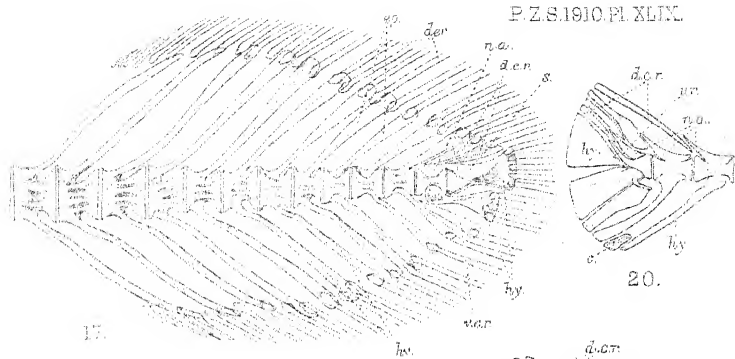


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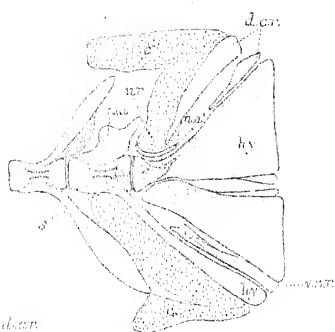


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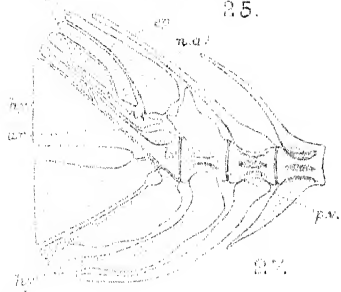
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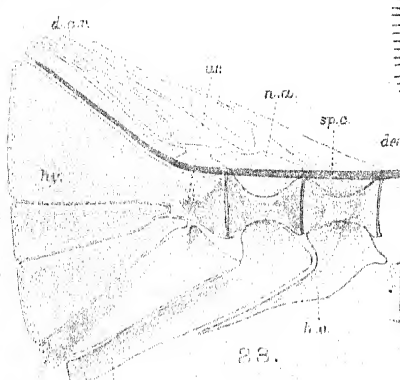




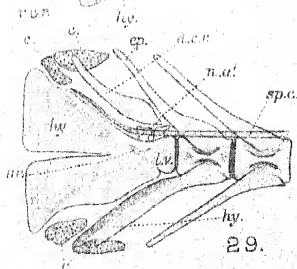
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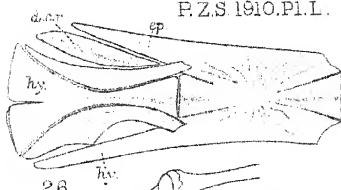
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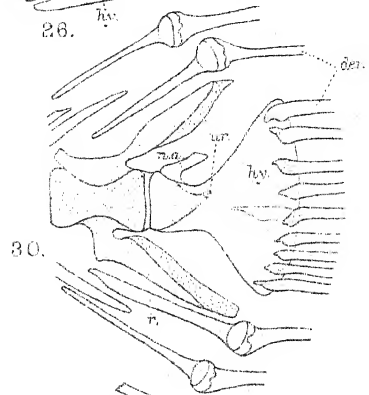
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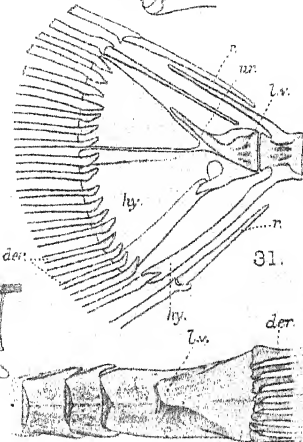
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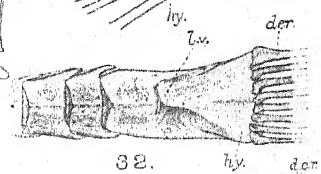
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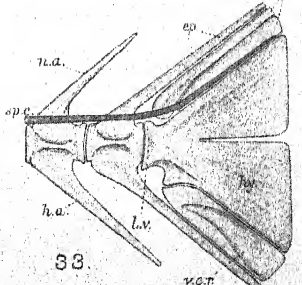
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R.H. Whitten and

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CAUDAL FINS OF TELEOSTOMI.



at the Naples Zoological Station. The many friends who have supplied me with material and suggestions also have my best thanks. For the identification of most of the species I am greatly indebted to Dr. Lo Bianco of the Naples Zoological Station. Lastly, I am deeply grateful to the Birmingham Natural History and Philosophical Society and others, for grants without which the work could scarcely have been done.

The dissections have been carried out as carefully as possible under the microscope, and it was found necessary in most cases to render the specimen transparent by some clearing agent such as turpentine or xylol, in order to see exactly how the vertebral column ended, and to clear up any other doubtful points.

In reviewing the literature on the subject of caudal fins, the very numerous casual references must be omitted for the present. Perhaps the earliest definite work relating to fishes' tails is that of Agassiz in 1833, in which the author recognized two types of caudal fin, the heterocercal and homocercal; the former term still retains its original meaning, but the latter was only used to indicate an externally symmetrical fin as distinguished from the asymmetrical heterocercal form. In a geological contribution by McCoy in 1848, the term "diphycercal" first appeared to designate the truly symmetrical caudal fin; it is interesting to note that Cope in 1871 coined the term "isocercal" to mean the same thing, in ignorance, as that author states, of McCoy's paper. Stannius, in a text-book on the Vertebrata, published in 1854, gives considerable attention to the tail-fin; he refers to a very large number of Teleosts, but with questionable accuracy. The most interesting feature of his remarks concerns his belief, which seems to be true, that the supports of the fin-rays are formed of arches and radials fused; *Belone* is quoted in support of this view.

But it was in 1859 that Huxley first gave a correct description and interpretation of the homocercal tail; he exposed the false symmetry of form in *Gasterosteus*, and traced its development. It is unfortunate that the promised account of the development of the eel's tail never appeared, for the slight reference made to this form is of doubtful accuracy, due, no doubt, to only a superficial examination. Very soon followed (in 1860) an excellent essay on caudal fins among Ganoids and some Teleosts by Kölliker, accompanied by valuable figures which have been reproduced almost universally since. Lotz followed in 1864 with a paper containing little new work.

A revival was given to the subject in 1878 by Alex. Agassiz in a short paper on the development of the tail of the flounder; his remarks had the effect of raising the important question of the true morphology of the homocercal caudal fin. In 1882, E. T. Newton read a paper on "Fishes' Tails" before the Quekett Microscopical Club; this consisted of a general review of past work, together with a description of the tail of the sprat; the paper included an incorrect figure of the caudal fin of the cod.

The most comprehensive work of all, however, was published by Ryder in 1886; on the whole, it contained very useful information, but his figure of the tail of the young eel is wrong with respect to the neural arches. Ryder's suggestions on the origin of heterocercy are interesting and probably correct, though somewhat novel. Ryder's evolutionary series of the forms of the caudal fin has come to be acknowledged as the order of appearance of the different types in time. The next work of importance dealing with caudal fins of fishes was written in 1895 by Dollo in discussing the phylogeny of the Dipnoi: basing his conclusions on geological evidences, he gives the term *gephyrócercy* an extraordinarily wide application; this arises from the idea, strongly upheld by Dollo, that the present caudal fin in many Teleosts is really a posterior anal fin, brought into its present position by complete atrophy of the real caudal. Dollo's is the last of important references regarding the tail-fin.

Boulenger, in 1901, in dealing with the fishes of the Congo, gave a good summary of work done. In 1907, Gregory, in his work on the classification of Teleostomous fishes, makes continual references to the caudal fin; but it is difficult to reconcile many of his statements: for instance, the caudal fin of *Mastacembelus* is referred to as *gephyróceral*, while in fact internally it is quite a generalized homocercal type. As an appendix to the work, there was given an elaborate scheme of the evolution of the caudal fin, which includes several new terms, considered by some as unnecessary.

## 2. TERMINOLOGY.

In order to avoid any ambiguity, I have thought it necessary to modify the meaning of several terms; some have been widened and others have been more restricted as regards their denotation. The reasons for such modifications are given in their respective paragraphs:—

1. *Urostyle*.—This term is used in the generally accepted sense denoting the more or less elongated cone-like termination of the vertebral column, appearing as a prolongation of the last centrum. It represents the fusion of several centra.
2. *Hypaxial*.—This adjective refers to any structure morphologically ventral to the chordal axis.
3. *Epaxial*.—This adjective refers to any structure morphologically dorsal to the chordal axis.
4. *Hypural*.—Any hypaxial element having a direct connection with the chordal axis, and bearing one or more fin-rays distally, will be called a hypural or hypural bone. Previously, this term has been used rather loosely and in such a way as to leave one in doubt as to its limitation; the limitation given above, concerning its direct connection with the chordal axis—*i. e.* as a general rule, with centra—as will be seen later, both widens and narrows the meaning of the term.

5. *Epural*.—This term may be regarded as applying to the dorsal homologue of the ventral hypural, *i. e.* any epaxial element, having direct continuity with the chordal axis, and bearing one or more fin-rays at its distal end, will be called an epural or epural bone. It is only after the most careful consideration that I have decided to change the definition of this term. It was established by Huxley in 1859, and appears to have been used by him to indicate those isolated ray-bearing bones situated immediately dorsal to the urostyle in *Gasterosteus*. The change suggested is based solely on my conclusions respecting the real morphological value of the several fin-ray supports, and, reluctant as I am to make any changes in established nomenclature, I believe the reader will agree that the subject will be much simplified by the change.
6. *Radial*.—The term radial is used in its usual sense as synonymous with "interspinous bone" and "somactid" of some writers; it implies a more or less dagger-like bone, primarily having no direct continuity with the vertebral column, and supporting distally one or more fin-rays.
7. *Last vertebral segment*.—This term will refer to the last centrum plus urostyle, if such exists. The last centrum is never perfect, and is often no more than a cone, the apex of which is directed posteriorly.

### 3. MORPHOLOGY OF CAUDAL FIN.

This section will be descriptive of a selection of caudal fins, and the order in which they are dealt with corresponds essentially with the classification given by Sedgwick in his 'Text-Book of Zoology.' Owing to lack of time and material, the series is not as complete as one would wish; for example, only the Siluridae among the Ostariophysi receive attention, and the Symbranchii are completely omitted. Except for these sub-orders, however, the types are fairly representative of the others, at least of the Teleostei. Almost every example taken presents interesting features, but owing to the impossibility of including, in the present paper, figures of all the species treated, only the barest description of many forms can be attempted at present.

ACIPENSER STURIO. (Chondrostei, Acipenseridae.) (Plate XLVII. fig. 2.)

The Sturgeon presents a definitely heterocercal tail; the end of the caudal axis from the root of the tail-fin is directed upwards, and the ventral lobe is enlarged, producing a very unsymmetrical fin. No centra are formed from the notochordal sheath. The ventral lobe of the fin is supported by a very regular series of hypurals; the name hypural has been applied here, since these structures strictly comply with the definition. They are of particular interest, because, in the anterior part of the fin, where they are most strongly developed, they exhibit a definite segmentation: the largest show four successive segments (*h. a., p., m., and d.*,



in the figure); proceeding backwards, as they become smaller, three segments are shown, then two, and finally only one can be traced. This segmentation is due, I believe, to the formation of the hypural by the coalescence of radial with hæmal arch; anteriorly, the three segments, the proximal (*p.*), median (*m.*), and distal (*d.*), of the radials are present, the distal still remaining free; from before, backwards, the fusion becomes more perfect and finally all trace of it is lost. This composite nature is a feature which substantiates the claim of these hypaxial supports to the title hypural. The dermatrichia constituting the ventral lobe considerably overlap their endoskeletal supports. Dorsally, the arches (*n.a.*) and radials (*d.e.r.*) remain distinct throughout the fin and are less regular than the hypaxial elements. The dorsal radials are almost hidden from view by the forking proximal ends (removed in the figure) of the stout fulcra which fringe the margin of the dorsal lobe. The whole of the elements at the extremity of the tail are hidden by the dermatrichia.

POLYODON SPATULA. (Chondrostei, Polyodontidæ.) (Plate XLVII. fig. 3.)

Externally the tail of *Polyodon* is very deceptive; its symmetry of form is most marked, and it resembles in outline the deeply cleft tail of some Teleosts. It is well-known, however, that on dissection it proves to be an excessively heterocercal type, the caudal axis being directed upwards and extending to the extremity of the dorsal lobe. No centra are formed. Almost throughout the tail-fin the neural arches (*n.a.*) are single elements, and are somewhat irregular in size, particularly towards the extremity of the axis. Resting upon these arches are the radials (*d.e.r.*); the first four or five are slender in build, but almost throughout the fin they resemble the neural arches themselves. They, too, are very irregular both in disposition and size, and here and there they show signs of having been more numerous formerly. The various elements at the extremity of the axis are difficult to distinguish, owing to their small size and tendency to fusion; the same difficulty is experienced ventrally in this region. The radials are the immediate supports of the fulcra (*f.*).

Turning to the ventral elements, a very regular series presents itself, in striking contrast to the dorsal side: there is a regular series of hypurals, very large at the root of the fin where the large dermatrichia of the ventral lobe are supported. As in *Acipenser*, very many of these hypurals show distinct segmentation, thus giving evidence of being composed of four successive elements, the distal of which, in the case of the first seven supports, is distinct and separate. The interpretation seems to be that each hypural is composed of hæmal arch and radial fused, the tri-segmental nature of the latter being retained in several cases. Naturally the best examples of this are given by the anterior hypurals, where the supporting elements are larger. The tri-segmental arrangement gradually gives way to a bi- and finally a uni-segmental

structure in passing from before, backwards. The caudal fin of *Polyodon*, then, is obviously heterocercal, but of a more specialized type than *Acipenser*, on account of its nearer approach to the homocercal type.

AMIA CALVA. (Holostei.) (Plate XLVII. fig. 4.)

The caudal fin of *Amia* is externally symmetrical, or at any rate the discrepancy in symmetry is very slight indeed, and negligible. But dissection reveals a very unsymmetrical internal structure; at the root of the fin the vertebral column takes a sudden turn upwards, at a considerable angle. The centra are well formed and retained throughout the length of the axis, and consequently no urostyle is present. Nearly the whole of the dermotrichia are supported by hypurals, a feature which it shares with the majority of Teleostean fishes; these hypurals are slightly expanded or somewhat club-shaped at their distal ends, and each bears a single fin-ray. The last three hypurals belong to the last centrum, but each of the other centra possesses but one hypural. The final dorsal element (fig. 4, *n.a*!) is strikingly large, and continues beyond the vertebral axis for some distance between the fin-rays. Kölliker remarks that it is cartilaginous and contains the spinal cord: he regards it as an incorporation of vertebræ and neural arches. In the specimens I have examined, the same structure proved to be bony, and grooved along the dorsal edge to conduct the spinal cord; it appears to correspond to a bone, frequently found among the Teleostei, which I have regarded as a persistent neural arch, retained, even when its adjacent homologues are suppressed, as a protection for the delicate termination of the spinal cord. According to Kölliker, there are three dorsal caudal radials (*d.c.r.*) remaining as supports for the insignificant fin-rays which constitute the epaxial contribution to the caudal fin; but these dorsal radials are very poorly developed. Most authorities agree that the caudal fin of *Amia* is scarcely correctly described by being called heterocercal, and therefore it is generally referred to as hemi-heterocercal. So near, however, does the structure approach homocercy that hemi-homocercal would probably be a more suggestive designation: however that may be, the fin may certainly be considered the most specialized type of heterocercal forms.

*General remarks on the Ganoid Caudal Fin.*

It has been thought advisable to omit any detailed references to other Ganoids than the three considered, for the present, since they have not been cleared up to my entire satisfaction and material is lacking. But the Ganoid caudal is characteristically heterocercal; truly protocercal forms are absent, and homocercy is nowhere attained within the group. The three types considered illustrate how the tendency of specialization is to approach the homocercal condition; in *Acipenser*, the typical heterocercal form, so characteristic of the Elasmobranchs, is present; *Polyodon*, by

an increase in the size of the ventral lobe reaches a step towards the externally symmetrical homocercal fin; while *Amia* proceeds furthest of all in the homocercal direction, requiring but one single feature, the possession of a true urostyle, to attain the homocercal condition.

## TELEOSTEI.

### MALACOPTERYGII.

#### MORMYRUS KANNUME. (Mormyridæ.)

In general, *Mormyrus* provides a type of homocercal caudal fin by no means generalized. The last two or three vertebrae are directed slightly upwards. The urostyle is absent or fused completely with a hypural bone; such an advanced homocercal feature as this is not consistent with the position of *Mormyrus* as one of the least specialized of Teleosts, a position assigned to it according to general characters. In respect to the hypurals, uncommon features are shown: in the first place the last centrum presumably is fused with the last hypural but one, instead of the last as is usual: again, two hypurals are attached to the penultimate vertebra and the anterior of these is exceptionally large. It is important to notice that only two hypural bones are associated with the last vertebral segment—the small number being another feature of the specialized homocercal caudal. The epaxial elements are interesting; the neural arch to the last centrum is strongly developed; it is pierced throughout by the spinal cord which is continued beyond the arch among the dermotrichia. It will be remembered that a similar condition of the last neural arch was found in *Amia*. The neural arch of the penultimate vertebra is very much reduced, and the antepenultimate vertebra bears an epural bone.

#### ENGRAULIS ENCRASICHOLUS. (Clupeidæ.)

The Anchovy provides an illustration of one of the least specialized of homocercal caudal fins. No centra enter into the upturned part of the caudal axis. The notochord is prolonged beyond the long urostyle, but except for the extreme end which extends among the dermotrichia, it is protected by several slender and closely fitting ensheathing bones which it is difficult to homologize. Dorsally and ventrally at the end of the notochord is a delicate cartilage, each, it may be, a vestige of once functional neural or hamal arches; such vestiges are referred to by Ryder as opisthural cartilages. The hypaxial endoskeletal supports of the fin-rays are nine in number, seven of which belong to the last vertebral segment. It is a little difficult to decide whether the term hypural is correct for all these supports, as some, at any rate, appear to be ventral caudal radials only; however, it will be better for the present to call all of them hypurals. This fish possesses the largest number of hypurals (viz. seven) to the last

vertebral segment which has been found. The dorsal contribution to the caudal fin is comparatively small. Of the last four vertebrae all but the last bear epural bones and the last appears to have its neural arch greatly reduced. The most posterior of the epaxial fin-rays are supported by two or three poorly developed dorsal caudal radials; the proximal ends of these radials are almost in contact with a triangular cartilage applied to the dorsal side of the notochord near the termination of the urostyle; this cartilage probably represents a vanishing neural arch.

CLUPEA PILCHARDUS. (Clupeidæ.) (Plate XLVII. fig. 5.)

The caudal fin of the Pilchard very closely resembles that of the Anchovy. The urostyle (*ur.*) is long and slender, and the notochord (*n.*) is produced beyond it, but not beyond the distal ends of the endoskeletal supports. An opisthural cartilage (*o.c.*) is attached to the end of the notochord, and extends between the dermatrichia. Nine hypural bones are present, seven of which belong to the last vertebral segment, as in *Engraulis*; the hypurals vary considerably in size. Epaxially, the dermatrichia are supported by two epurals (*ep.*) and three dorsal caudal radials (*d.c.r.*); the latter are short bones situated between the last epural and the notochord. Proximally the dorsal radials about a triangular bone (*n.a.*<sup>1</sup>)—cartilage in *Engraulis*—on the dorsal side of the urostyle: this triangular bone probably represents one or more neural arches of vertebrae now absorbed into the urostyle. The last centrum (*l.v.*) is provided with a large spatulate neural arch (*n.a.*) peculiarly constricted at its proximal end.

Comparing the caudal fins of the two Clupeoids here described and also that of the Sprat as detailed by Newton, it will be seen that there is a striking similarity throughout; the figure given in Newton's paper is that of a young *Clupea sprattus*, and the urostyle is seen to be composed of several centra which, no doubt, are also present in *C. pilchardus* and *Engraulis encrasicolus* in the young, but which are obliterated in the adult. All show a lowly specialized homocercal form, approaching very closely the *Amia* type.

NOTOPTERUS BORNEENSIS. (Notopteridæ.) (Plate XLVII. fig. 6.)

This fish is provided with a highly specialized caudal fin, and also presents one or two peculiarities. The caudal is continuous with the ventral median fin, but the caudal proper may here be limited to that part composed of dermatrichia which are attached to the endoskeleton by means of a proximal forking, as distinguished from the ball and socket nature of the attachment of the anterior fin-rays to the radials. Thus the caudal fin is supported by three hypurals and one epural; hence it is not strictly hypocercal as Gregory states. No urostyle can be seen in the dissection, and even clearing fails to give any certain clue as to its exact outline in the substance of the last hypural bone, and what

may be at first considered a urostyle, indicated by a ridge along the dorsal side of the hypural, has a companion ridge directed ventralwards; the loss of the urostyle or its fusion with a hypural bone is an advanced character. A large hypural bearing four dermotrichia is attached to the penultimate vertebra, while that of the antepenultimate supports only one. An interesting feature in this caudal fin is the epaxial fin-ray support; this consists of a single epural bone broadly expanded distally, and attached to the penultimate vertebra. Such an expanded epural is quite unusual in caudal fins, and I know of no other instance.

*General remarks on the Malacopterygii.*

The examples chosen illustrate how varied the caudal fin structure may be, even in a single sub-order of Teleosts. Two extreme types are met with: the Clupeoids, by the extension of notochord beyond the bony axis, by the vestiges of once functional arches in the form of opisthural cartilages, and by the large number of hypural bones to the last vertebral segment, provide an example of a lowly specialized form of caudal fin; while *Notopterus*, by the loss of the urostyle and the reduction of the number of hypurals to the last vertebral segment to a single bone, is an example of a highly specialized form.

OSTARIOPHYSI.

CLARIAS sp.? (Siluridæ.)

Only a single specimen of this fish has been procurable, but the caudal fin appears to be quite normal. The tail-fin is fully differentiated although the dorsal and ventral fins reach nearly to the end of the body. Internally the skeleton is remarkable in presenting a very long urostyle, longer than that of any fish examined, extending posteriorly as far as the distal ends of the hypurals; it does not appear to be actually fused to a hypural. The hypaxial part of the fin is supported by five hypural bones, four of which are associated with the last centrum and urostyle, and also by one ventral caudal radial occupying the space between the first and second hypural bones. The hypural of the penultimate vertebra has the appearance of being formed by the coalescence of a radial and a hæmal arch. The epaxial fin-rays are borne by one epural bone belonging to the last vertebra but one, and also by a dorsal caudal radial between the epural and the urostyle. The spinal cord can be traced to the end of the urostyle. The final centrum possesses the vestige of a neural arch, through which the spinal cord passes.

Here then is a generalized type of homocercal caudal fin, for in it are representatives of all possible endoskeletal supports, viz., hypurals, ventral caudal radial, and dorsal caudal radial, and besides, it possesses a well-marked urostyle.

*Plotosus* sp.? (Siluridæ.) (Plate XLVII. fig. 7.)

The caudal fin of *Plotosus* is very interesting and very simple; it forms part of a continuous median fin and terminates a gradually tapering tail. All the specimens examined were from Torres Straits and were presented to me by the late Professor Bridge. They were all young, but the skeletal elements were quite fully established. Before entering into a description of the fin, it will be instructive to call attention to the remarks made by Mr. Tate Regan before the Zoological Society on April 28th, 1908, concerning the caudal fin of *Unidoglanis megastomi*, also a member of the Plotosinæ. He writes:—

“The Siluroid fishes of the subfamily Plotosinæ have been generally defined as having two dorsal fins, a short anterior one and a larger posterior fin continuous with the caudal, similar to the long anal. The so-called second dorsal proves to be a procurent portion of the caudal fin which has extended forward along the back, and, in the species exhibited, has a base of more than two-thirds the total length of the fish, and is formed of about 130 rays; these are supported directly by the neural spines, in striking contrast to the externally similar anal fin, the rays of which are attached to a series of interhæmals.” Presumably interhæmals are synonymous with radials.

On examining *Plotosus*, which is a very close relative, I was pleased to find that the same characters were exhibited in both cases, or, I believe, practically the same, for although in *Plotosus* the rays of this “procurent caudal” are not actually attached to the neural spines but interdigitate between them, they have no other endoskeletal support, as the anal rays have.

Now, the conclusion to be drawn from the above quotation is that Mr. Regan would define a caudal fin as that part of the median fin system which is directly supported by hæmal or neural spines, or in the language adopted in this paper, by hypurals and epurals alone. It must be pointed out, however, that fin-rays of true caudal fins are frequently supported by undoubted radials, in addition to hypurals and epurals, and interdigitating between these supports; throughout the Gadidæ this is the case, many Acanthopterygii show the same thing, as also does *Clarias* just considered. But I fully agree with Regan's remark that the so-called second dorsal fin is part of the caudal, but for an entirely different reason. I hope to deal with the definition of the caudal fin at a future time after my observations have been more extended; but for the present, in connection with this discussion I base my agreement with Regan's conclusion on the nature of the fin-rays themselves, and not on their endoskeletal supports. The dermotrichia of the caudal fin differ from those of the remainder of median fins in the method of attachment to their internal supports; the caudal fin-rays of Teleosts attach themselves by means of a forking at their proximal ends, while those of the dorsal and anal fins are provided with a kind of socket by which they are attached to the distal segment of the radial. So far as

I am aware, this difference is universal among Teleosts, but, as stated above, as yet I do not assert it to be without exception. The matter is called attention to, in order to make it quite clear that fin-rays of a caudal fin may be supported directly by undoubted radials.

Concerning other features of the caudal fin of *Plotosus*, the last dorsal ray is supported by an epural which is attached to the penultimate vertebra, and which shows the union of two elements, a radial and a neural arch. Hypaxially is a large hypural firmly united with the urostyle, and bearing ten dermotrichia. In the specimen figured the penultimate centrum possesses two ventral appendages, a hypural supporting one ray, and a haemal arch. Curiously enough, the next anterior ray is without a support and seems to anticipate a similar state of affairs ventrally as dorsally: such, however, is not the case, for each ray preceding is a typical anal fin-ray supported by a true radial.

Hence the caudal fin of *Plotosus* is a very highly specialized organ, totally different from the preceding type, *Clarias*.

SYNODONTIS SCHALL. (Siluridae.) (Plate XLVII. fig. 8.)

The last six vertebrae form the basis of support for the deeply cleft caudal fin in this fish. The urostyle is lost and the last centrum is firmly fused to the last two broad hypurals, which occupy a terminal position. The hypaxial fin-rays are mainly supported by these two hypurals, but in addition there are five others, one to each of the preceding five vertebrae; these two hypurals afford excellent evidence of the coalescence of radials and haemal arches in their formation. Epaxially are four epurals, one to each of the four vertebrae preceding the last two; these epural bones, like the hypurals, show the duplicate nature well; it will be seen that the neural arch of the penultimate vertebra and its corresponding radial have not fused, but a little forward movement and then the fusion with the neural arch, on the part of the radial, would produce an exactly similar structure to the preceding epurals. This caudal fin provides one of the best illustrations of the fusion of radials with arches in the formation of epurals and hypurals. Needless to say the fin is a highly specialized homocercal type.

*General remarks on the Siluridae.*

The single family Siluridae, therefore, includes great diversity in the form of the caudal fin structure, from a very generalized to a highly specialized type.

APODES.

ANGUILLA VULGARIS. (Murænidae.)

Having obtained a good series of stages, I have been able to trace the development of the caudal fin in *Anguilla* from the *Leptocephalus* stage to the adult.

1. *Leptocephalus brevirostris*. (Plate XLVIII. fig. 9.)

It is perhaps somewhat unfortunate that in the *Leptocephalus* all essential skeletal structures are already present; in fact, there is very little difference between it and the elver four inches in length. There is very clearly shown a comparatively long urostyle slightly directed upwards; this urostyle is not fused with the hypural bone immediately ventral to it. In my specimen this hypural, the distal end of which extends beyond the urostyle, was already a single cartilage, though in older specimens, a very distinct cleft was frequently to be seen. Three of the four fin-rays attached to this hypural were bifid distally, though I believe the number of distally bifurcated rays is a matter of accident. The penultimate vertebra carries the characteristic U-shaped hypural of the Apodes, representing two pieces fused proximally. The antepenultimate vertebra is a double structure, and carries two haemal processes, the posterior of which bears a fin-ray and shows a definite trace of being formed by the union of a radial and a haemal arch; this has already been drawn attention to by Ryder. The double vertebra mentioned is not, as Ryder seems to suggest, a constant feature, but certainly is very common. Dorsally, no epural bones are present; every ray is supported by a radial. In the only figure of the caudal fin of a young eel I am aware of, namely that of Ryder's, the neural arches are not truly represented; in reality they are rectangular plates, equal in length to the vertebrae to which they are attached; even the last retains its rectangular shape, covering up urostyle and overlapping the last hypural to some extent. The spinal cord can be traced even among the fin-rays beyond the distal end of the last hypural; this fact is evidence of considerable abbreviation.

2. *The Elver*. ( $4\frac{3}{4}$  ins. or about 12 cm. long.) (Plate XLVIII. fig. 10.)

This stage is next taken as being the last in which the urostyle can be traced; the last hypural has already encroached upon it dorsally, while in specimens five inches long it has vanished, and the last hypural and the last vertebral segment have become a single piece. Neural spines have appeared on all the neural arches except the last two, and a thickening indicative of a spine is seen there also. The spinal cord does not extend among the fin-rays as in the *Leptocephalus*. All other features are much the same as in the *Leptocephalus* stage, though naturally more pronounced.

3. *Common Eel—adult*. (Plate XLVIII. fig. 11.)

After the preceding stage, and sometimes earlier, the last two neural arches often fuse into one. But the main feature to be noted in the adult is the complete absorption of the last vertebral segment, including centrum and urostyle, by the last hypural; all efforts to reveal the urostyle by clearing agents have failed; the union is complete, hence, what appears in the adult to be hypural



only is in reality hypural plus the last vertebral segment. The distal arms of the U-shaped hypural of the penultimate vertebra often tend to fuse and so produce an elliptical bone. There is considerable variation in the number of fin-rays supported by the various terminal elements; the terminal dorsal and ventral radial may or may not support a ray. It is usual for the last two hypurals to support four rays each, but this too is liable to variation. In young animals it is quite accidental whether fin-rays bifurcate or not distally, and it is not safe to conclude, with Ryder, that bifurcated dermatrichia are caudal proper and others dorsal or ventral respectively.

CONGER VULGARIS. (Muraenidae.) (Plate XLVIII. fig. 12.)

In most respects the caudal fin of the Conger is similar to that of *Anguilla*. Only by the aid of clearing agents can the exact outline of the various elements be traced; when thus treated, it is seen that the vertebral column proper ends in a long cone-like vertebra, directed posteriorly in a straight line with the vertebral axis, *i. e.* there is no tendency to upturning, and a urostyle cannot be said to exist. But all this is invisible without the aid of clearing agents, and the last centrum appears to be merely the proximal end of the three hypurals, which in reality are firmly fused with the last centrum. However, any difficulty concerning the ending of the vertebral axis is removed by a reference to the young stages: a young conger of  $3\frac{3}{4}$  inches (9.5 cm.) length or less will show a condition of things very like those in *Anguilla*, viz., a urostylar process upwardly directed, and occupying a position along the proximal dorsal edge of the last hypural; in a specimen  $4\frac{1}{2}$  inches (or 11.5 cm.) long, this could not be seen in the mere dissection.

Those dermatrichia which may safely be called caudal are supported by four hypural bones: the first of these is attached to the penultimate vertebra, instead of the autepenultimate, as in *Anguilla*, and the remaining three are all fused to the last vertebral segment. In this respect, the Conger differs from the Common Eel in which only one belongs to the last centrum, and the next two (forming the letter U) to the penultimate vertebra: this may represent a further shortening of the vertebral axis in *Conger*. A word should be said here, calling attention to the excellent illustration afforded by these hypurals, particularly the first and second, of their double nature: a line of fusion can be traced across the hypural dividing the latter into two parts, the proximal of which is almost exactly similar to the preceding haemal arches, and the distal part is like a radial.

There are no epural bones. The neural arches closely resemble those of *Anguilla*, but are more simple, the anterior ones possessing a very feeble spine; the last, which is specially long, to protect the end of the spinal cord, possesses a peculiar bony process running in an antero-ventral direction across the last centrum; this is probably a process for the attachment of caudal muscles.

## MURENA HELENA. (Murænidae.)

The caudal fin of the Roman Eel is essentially similar to that of the Conger, and attention need only be drawn to the peculiarities presented. The hypural bones are attached to the last centrum. The spur-like process of the last neural arch, mentioned in *Conger*, is more pronounced and fuses with a posteriorly directed process of the first hypural bone. The posterior neural arches are very simple, having no spine, and the closely aggregated radials of the dorsal fin are in close contact with them. The hæmal arches very closely resemble the neural arches: the penultimate vertebra does not bear a hypural bone.

## MYRUS VULGARIS. (Murænidae.) (Plate XLVIII. fig. 13.)

The caudal of this fish is again similar to the preceding types. Only one hypural is attached to the last centrum, which is quite indistinguishable, appearing only as the proximal end of the hypural bone: only one hypural may be said to be attached to the penultimate vertebra, though it is clear that this has been formed by the coalescence of the distal ends of the arms of the U-shaped structure in other genera. The hæmal arches of the posterior vertebræ are of a horseshoe shape; this may account for the U-shaped hypural of the penultimate vertebra, which is so general in the family.

*General remarks on the Apodes.*

There is a striking uniformity in the structure of the caudal fin in this sub-order, due possibly to similar habits. In spite of observations, as early as Huxley's in 1859, to the contrary, writers repeatedly refer to the Eels as possessing diphyccercal or protocercal tails. It cannot be too greatly insisted on, that whenever an upturned urostyle is present, either in the adult or the larva, a tail is not protocercal or diphyccercal. Externally, of course, the Eels, with their undifferentiated median fin system, do present a primitive protocercal condition, but dissection proves the terminal endoskeletal supports to be very unsymmetrical; the broad hypural bones have no corresponding dorsal homologues. The caudal fin of the Apodes complies in all its essentials with the definition of homocercy, which will be discussed later; it cannot be called anything but an advanced form of homocercal caudal.

While dealing with the Apodes, it is interesting to note the references to the ancestral forms. The fossil *Urenchelys* from the Chalk beds has a homocercal tail—presumably an externally recognizable homocercal tail—and probably, therefore, much less specialized a form than the advanced form the modern Apodes have been shown to possess. Thus all that has happened is a steady process of specialization, exactly as is to be expected.

## HAPLOMI.

## GALAXIAS sp.? (Galaxiidae.)

Only a single specimen was available for examination; this revealed a free urostyle, beyond which the notochord continued for some distance, but did not reach the dermatrichia. Seven hypurals are present, five of which are attached to the last vertebral segment; the last three are closely applied to each other and so form a large plate. Dorsally the dermatrichia are supported by two epural bones and a dorsal caudal radial, the latter being cartilaginous. Both the epurals and hypurals of the penultimate and antepenultimate vertebrae are very broadly expanded, and show traces of the inclusion of radials in their formation. The last vertebra possesses a small neural arch and the spinal cord can be traced to the end of the notochord. Such a caudal fin must be considered a lowly specialized form of homocercy.

No generalizations can be made on the Haplomi until more species have been examined.

## HETEROMI.

## FIERASFER ACUS. (Fierasferidae.)

In this fish the median fins are continuous. At the extreme end of the tail no fin-rays are present in the fin-fold, so that there is a gap between the fin-rays of the dorsal and ventral fins. The vertebral column ends in a perfectly straight line, and, towards the end, consists of alternate segments of centra and notochord, the final element being notochord which comes in contact with the integument. The fin is therefore perfectly symmetrical externally and internally and moreover shows obvious signs of degeneration. Ryder concludes that the whole of the true caudal has been lost, and hence the tail is truly geophyrocercal. It is interesting to note that the developmental stages do not reveal any heterocercal tendencies.

FIERASFER DENTATUS. (*Echiodon dentatus*.) (Plate XLVIII. fig. 14.)

The figure of the tail of this species given by Emery is most interesting as presenting a typical geophyrocercal tail. The larva is provided with a long filamentous tail-ending, which is eventually lost in some way, and the adult tail gives the appearance of having had the end bitten off; the vertebral column ends in a vertebra exactly similar to the preceding ones; the dorsal and ventral fin-rays attempt to bridge over the gap caused by the loss of the caudal extremity, but never actually meet. The fin-rays of the dorsal and anal fins are supported by very small cartilages which represent radials, and which are far removed from the axis. I have not yet had an opportunity of examining this caudal fin, and so I reserve any remarks on this remarkable form.

*General remarks on the Heteromi.*

All fishes belonging to this sub-order, whether fossil or living, appear to be either eel-like or deep-sea forms; from this it is to be expected that the tail-fin when present is similar throughout, *i. e.* gephyrocereal.

## CATOSTEOMI.

## GASTEROSTEUS ACULEATUS. (Hemibranchii.)

The caudal fin of this fish was well described by Huxley in 1859. The vertebral column ends in a long urostyle which is fused along the dorsal edge of the last hypural bone. There is a small neural arch to the last centrum, which Huxley figures as being continuous with it, though there is a line of junction separating arch and urostyle. The penultimate vertebra possesses an epural and hypurals; between the epural and the urostyle is a dorsal caudal radial (the "epural" of Huxley).

## CENTRISCUS SCOLOPAX. (Hemibranchii.)

The urostyle here is suppressed and the "cone" of the last vertebra shows only the slightest suggestion of upturning. Two hypurals are attached and equally well fused to the last centrum. An epural and hypural are attached to the last vertebra but one, and both show well that they are composed of a neural and a haemal arch respectively, together with a radial. A single dorsal caudal radial is situated between the epural and the last hypural.

Thus the caudal fin of *Centriscus* is highly specialized in contrast with the nearly related form *Gasterosteus*.

## SYNGNATHUS ACUS. (Lophobranchii.) (Plate XLVIII. fig. 15.)

The caudal fin of the Pipe-fish presents a perfectly symmetrical appearance, but morphologically it is quite unsymmetrical since all the eight dermatrichia are supported by hypaxial elements consisting of two expanded hypural bones. Although the young stages show a distinct urostyle, this structure is absent in the adult. There are no complications of any kind and the whole caudal structure is exceedingly simple. The spinal cord can be traced to the distal end of the hypural bone. On account of the presence of a urostyle in the larva and the hypaxial nature of the fin, the tail must be classed as homocercal; moreover, it is a highly specialized form of homocercy.

## SIPHONOSTOMUS RONDELETHI. (Lophobranchii.)

Precisely the same structure is found in this species as in the preceding type, hence it is unnecessary to repeat the description. The similarity is no doubt associated with the similarity in habits of the two fishes.

## NEROPHIS OPHIDION. (Lophobranchii.)

This fish has lost its tail-fin probably on account of the prehensile function of the tail, but other species of *Nerophis*, e. g. *N. aquoreus*, do possess a very small one, which resembles that of *Syngnathus* in miniature.

## HIPPOCAMPUS BREVIROSTRIS. (Lophobranchii.)

The Sea-horse has no caudal fin in the adult, but the larva possesses a urostyle and hypurals, which degenerate, probably owing to the prehensile habits.

*General remarks on the Catosteomi.*

Of the three families of the Catosteomi (Gasterosteidae, Centriscidae, and Syngnathidae) types of which have been examined, the Gasterosteidae certainly are the least specialized, and the Syngnathidae the most so, while the Centriscidae occupy an intermediate position, as regards the structure of the caudal fin. This order corresponds exactly with the general classification based on specialized features as a whole: this bears out what is often seen elsewhere, that the caudal fin may be useful in classifying fishes among smaller divisions, though it may not be depended upon as a broad taxonomic feature.

## PERCISOSES.

## BELONE ACUS. (Scombresocidae.)

Only the smallest trace of a urostyle can be seen in the adult. There are six hypural bones in all, four of which correspond to the last vertebral segment; the most anterior of these four possesses a prominent bony process to which muscles are attached. The neural arch to the last vertebra is very large and protects the spinal cord which can be traced to the distal end of it. The epaxial fin-supports are liable to some variation: there are sometimes two, and at other times three dorsal caudal radials; when two are present, it is on account of the third (the most anterior) having fused to the neural arch of the antepenultimate vertebra and so constituting an epural bone: this point in itself is evidence as to the way in which epurals may be formed.

The variation exhibited here is probably what Stannius referred to, in 1854, when he quoted *Belone* as demonstrating the fact that the fin-ray supports may be of a double nature, i. e. arches plus radials. *Belone*, therefore, is interesting as being the fish in which this feature, so frequently met with elsewhere, was first seen.

The penultimate vertebra never appears to possess an epural, as the radial and neural arch are always separate.

On the whole the caudal fin of *Belone* attains to a fair standard

of specialization, particularly as regards the suppression of the urostyle; but at the same time the number of hypurals, viz. four, associated with the last vertebra is indicative of a comparatively low type of specialization. The proximal ends of the fin-rays embrace their endoskeletal supports so as to almost exclude them from view.

AMMODYTES TOBIANUS. (Ammodytidae.) (Plate XLIX. fig. 16.)

The last vertebra and last hypural are completely fused and thus there is no free urostyle. The hypaxial supports consist of five hypurals, four of which are attached to the last vertebra. The dorsal elements are somewhat complicated: lying between the single dorsal caudal radial and the last vertebra and hypural are four separate bones, through three of which the spinal cord passes; these three possibly represent neural arches, while the fourth may be a dislodged arch, or a spine detached from its arch. It is interesting to notice that fusion of these four bones into a single piece would form a large neural arch exactly as in *Belone*.

ATHERINA BAYERIL. (Atherinidae.)

A small but free urostyle is found here; connected with it and the last centrum are five of the seven hypural bones supporting the hypaxial dermatrichia. A small cartilage, situated between the distal ends of the first two hypurals, shares in the support of the anterior rays of the ventral lobe; this may possibly represent a radial, but it is doubtful. Dorsally the fin-rays are supported by two dorsal caudal radials and one epural bone, the latter attached to the antepenultimate vertebra. The neural arch of the last vertebra is very large and is composed of three bones; it affords protection for the end of the spinal cord. Thus *Atherina* possesses a fairly generalized caudal fin, lacking only a ventral caudal radial, though even this may possibly be represented by the small cartilage mentioned.

The development of the caudal fin in this fish is interesting as being almost identical, in the earlier stages, with that of the Flounder as figured by Agassiz, and shows very clearly the deep incision between the original and the permanent caudals.

MUGIL CAPITO. (Mugilidae.)

The urostyle is lost in the tissue of the last hypural bone; three hypurals in all are attached to the last vertebral segment; three dorsal caudal radials are present, the last of which is applied to the dorsal side of the last hypural. The neural arch to the penultimate vertebra is very much reduced. The anterior fringe of the ventral lobe of the caudal is supported by small cartilages; what these represent it is difficult to determine. The fin therefore may be classed as an advanced type of homocercy.

*General remarks on the Percosoces.*

This sub-order presents considerable diversity in caudal fin structure; *Atherina*, with its free urostyle and numerous hypurals attached to it, possesses a comparatively lowly specialized caudal, while that of *Mugil* is quite a specialized form. Arranged in ascending order of homocercy, the four genera will appear thus: *Atherina*, *Ammodytes*, *Belone*, *Mugil*, which arrangement does not correspond with that of general classification.

## ANACANTHINI.

*Macruridae*.—The fishes in this family possess no caudal fin; they are deep-sea forms and the body ends in a finely tapering tail.

## MOLVA VULGARIS. (Gadidae.) (Plate XLIX. fig. 17.)

The Ling possesses a simple type of Gadoid tail. No less than thirteen vertebrae contribute towards the support of the caudal fin; all of these vertebrae are provided with hypural bones (*hy.*) and all, except the last two, with epural bones too; special attention, therefore, need be directed only to parts connected with these last two vertebrae. The final vertebra possesses no urostyle, and is firmly fused with the broad last hypural which occupies a terminal position and bears five dermotrichia. That part of the last hypural which encroaches upon the dorsal side of the last centrum is seen in other Gadidae, e. g. *G. minutus*, to be a secondary extension of this bone, only appearing late in development; in young stages the hypural is totally ventral to the centrum. The hypural bone of the penultimate vertebra is also broadly expanded and bears three fin-rays. Between this hypural and the next anterior one is a ventral caudal radial (*v.c.r.*), in no way fused with any other skeletal element. Most of the hypural bones show signs of being formed by the coalescence of hemal arch and radial, the line of fusion being specially prominent after clearing agents have been used; the shading in the figure is intended to show this.

Epaxially, it is interesting to note the great reduction of the neural arch of the penultimate vertebra; that of the antepenultimate contributes to the formation of an epural bone. Between this last epural and the dorsal side of the last hypural are two dorsal caudal radials, each bearing a fin-ray; these radials never fuse with the neural arch, but always remain perfectly free. It will thus be seen that the caudal fin of *Molva* is not symmetrical internally and that the hypaxial fin-rays outnumber the epaxial; it is in every way consistent with homocercy, and its terminal skeleton with a very highly specialized type of homocercy.

## GADICULUS ARGENTATUS. (Gadidae.) (Plate XLIX. fig. 18.)

This small Gadoid possesses a more generalized caudal fin than does the preceding type; this is due solely to the presence of a

large number of radials in addition to the epural and hypural bones. Except for the fact that eleven vertebrae form the basis of support for the fin instead of thirteen as in *Molva*, all remarks made in reference to the latter genus apply equally to *Gadiculus*. The whole interest in this tail-fin lies in the radials; in addition to the epurals no less than six are present epaxially, and ventrally three are to be seen alternating with hypurals. Moreover, these radials may be either quite free, like ordinary radials, or they may be more or less fused with the neighbouring hypurals or epurals. This affords one of the strongest cases for the theory that hypural bones are formed by the coalescence of radials with hæmal arches. In the other median fins two radials are present between successive vertebral arches; thus probably the hypurals and epurals of the caudal have already absorbed one radial and the tendency is to effect a fusion of the second also. There can be no doubt about these radials being true radials and not a second neural or hæmal arch, since they never reach the centrum itself and never embrace the spinal cord or hæmal vessels at their proximal ends, as they would do if they were arches. The spinal cord can be seen to extend to the distal end of the last hypural bone. This caudal also is therefore a homocercal form.

#### *General remarks on the Gadidæ.*

There seems to be a certain amount of misconception among writers concerning the caudal fin of the Gadidæ; one or two quotations will make this clear. J. T. Cunningham, in 'Science Progress,' 1897, says:—"The structure and development of the tail described above (heterocercy) occur in the flat fish, but are entirely wanting in the Gadidæ. In the latter the tail is permanently diphyccercal and is composed of dorsal and ventral rays which are equal in number and size, and, in fact, closely resembles the tail of the extinct Oelacanthidæ. There can be little doubt that even if the Gadidæ cannot be directly derived from the latter family, they are descended from Crossopterygian Ganoids with diphyccercal tails and have never passed through a heterocercal condition." And Boulenger, in the Ann. & Mag. Nat. Hist. x. 1902, writes:—"I have reason to believe that Gadoids must have been derived from such a group as the Berycidæ, through forms of which the Macruridæ with thoracic ventral fins composed of seven to twelve rays are the nearest known examples, and in which the caudal fin has entirely vanished. I regard the isocercal condition of the Gadidæ as the result of the formation of a new caudal fin, the homocercal extremity of the vertebral column having been lost by the direct ancestors of these fishes." The same writer in comparing the caudal fin in the Pleuronectidæ with that of the Gadidæ says: (in the Pleuronectidæ) "the tail, whenever a caudal fin is well developed, belongs to the homocercal type (heterocercal in the embryo) with comparatively few rays (20 or less),"—thus differing from the Gadoids.



Other references might also be quoted, but these will be sufficient to show what misconceptions are held. Dealing with Cunningham's remarks first, a reference to either of the two figures given will show at a glance that the tail is not "permanently diphyccercal" and is not "composed of dorsal and ventral rays equal in number." In all, eight different species have been very carefully examined, and any of the following remarks apply equally to all; there are always more hypaxial fin-rays than epaxial; this is due to the fact that a broadly expanded hypural bone is attached to the last centrum. Thus the tail is a highly specialized homocercal form.

This author has apparently never been fortunate enough to secure young forms of Gadidae for detailed examination of the caudal fin structure or he would never have said that during the development the heterocercal stage is "entirely wanting."

*Gadus minutus* of one inch length shows an upwardly directed urostyle along the dorsal edge of the last hypural as clearly as in the flat-fish; this becomes much reduced in the adult and is in fact almost completely lost; and since the extremity of the vertebral axis is almost precisely the same in all adult Gadidae, it is quite reasonable to suppose that the young forms in every case are similar to *G. minutus*. Cunningham's error in this connection led him to suppose that the Gadidae "are descended from Crossopterygian Ganoids with diphyccercal tails and have never passed through a heterocercal condition." The latter statement, however, falls through.

Assuming Cunningham to be correct as regards the diphyccercal condition, Boulenger comes to the conclusion that the Gadidae are descended from a homocercal form, such as the Berycidae, but that homocercy was entirely lost, and the "isocercal (i.e. the diphyccercal) condition . . . is the result of the formation of a new caudal fin." But development proceeds just as in any highly specialized homocercal form, and hence the caudal fin of the Gadidae cannot be considered a new thing.

The caudal fin of this family further conforms to advanced homocercy in the great reduction of the neural arch of the penultimate vertebra; in all previous figures of the Gadoid tail, the last vertebra but one is shown bearing an epural bone; but in all the Gadidae examined, this has proved not to be the case; immediately dorsal to the penultimate vertebra there are always two dorsal caudal radials perfectly free and never fused with any other part of the neighbouring skeleton. Hypaxially, the same vertebra always bears a hypural bone.

Thus the caudal fin of the Gadidae is undeniably a specialized form of homocercy.

#### ACANTHOPTERYGII.

A preliminary note will be necessary before entering into details of the types chosen in this sub-order. In many forms in which a free urostyle is present, there is a fin-ray support

which occupies a position exactly in line with the urostyle; a difficulty comes about, therefore, in determining whether this element is hypaxial or epaxial. In shape it closely resembles the dorsal caudal radials, but the spinal cord runs along its dorsal edge; it may therefore be considered a dorsal caudal radial which has moved ventral to the spinal cord; but its present position below the spinal cord makes it possible also that it is a hypural bone, or perhaps a ventral caudal radial. For the present, however, I have decided to call it a hypural in order to simplify description, but the reader may consign it to any of the three suggested classes he may consider desirable.

SERRANUS CABRILLA. (Perciformes, Serranidae.) (Plate XLIX. fig. 19.)

The vertebral column ends in a well-developed and free urostyle (*ur.*), which is about the length of an ordinary vertebra. Six hypural bones (*hy.*) of varying size are associated with the last vertebral segment; the most anterior of these possesses a long spur-like process, running parallel with the urostyle, and undoubtedly functioning as an attachment for muscles; the last hypural is in direct line with the axis of the urostyle. Between the distal ends of the hypurals of the second and third last vertebrae is a small cartilage (*c.*) which shares the support of the smaller anterior ventral caudal fin-rays. Dorsal to the urostyle and extending beyond it, is a slender splint-like bone (*n.a.*) protecting the delicate end of the spinal cord; this probably represents one or more neural arches of vertebrae now absorbed into the urostyle. Independent of this bone, the last vertebra (*l.v.*) possesses a neural arch of its own; the neural arch of the penultimate vertebra (*p.v.*) is much reduced, and the antepenultimate vertebra is provided with an epural bone (*ep.*). Three dorsal caudal radials (*d.c.r.*) support the majority of the epaxial fin-rays.

This caudal fin, therefore, is a fairly typical form of a comparatively lowly specialized homocercal type.

CEPOLA RUBESCENS. (Perciformes, Cepolidae.)

This fish possesses a long tapering form of tail. The urostyle is prominent though slender; four hypural bones are attached to the last vertebral segment, the last overlapping the urostyle slightly. All the dermatrichia of the caudal fin are hypaxial, though epaxially there is a bone, not actually supporting a ray, which might be called a radial. Externally the median fin system appears to be a continuous one, but closely examined, there is to be found a very distinct and separate caudal. All the skeletal structures in the terminal end of the tail are very delicate and loose, the neural and hæmal arches not being actually fused with the elongated centra. The tail-fin is, however, definitely homocercal.

*CANTHARUS VULGARIS.* (Perciformes, Sparidae.)

The urostyle is well marked and free, and four hypurals are attached to the last vertebral segment; in all there are six hypurals, the second and third last vertebrae each bearing one. Epaxially, there are three dorsal caudal radials, and one epural which is attached to the antepenultimate vertebra. The neural arch of the penultimate vertebra is reduced. Between the last dorsal radial and the last hypural is a splint-like bone, the proximal end of which rests on the dorsal end of the urostyle; it protects the ending of the spinal cord and is probably a neural arch. The fin, therefore, is homocercal.

*BOX SALPA.* (Perciformes, Sparidae.) (Plate XLIX. fig. 20.)

The urostyle is well marked and distinct. Corresponding with the last vertebral segment are three hypurals, two of which are large, and the most anterior is provided with a ridge for the attachment of muscles; there are five hypural bones in all; between the distal ends of the first two is a small cartilage bearing a few of the small anterior hypaxial rays; a very small similar one is present on the anterior side of the first hypural. Epaxially, there are three dorsal caudal radials (*d.c.r.*), while the antepenultimate vertebra bears an epural bone; this epural is particularly interesting from the fact that in an animal 4 cm. long (fig. 20) it is seen to be two distinct and separate pieces—a neural arch, exactly similar to that of the penultimate vertebra, and a long cartilaginous radial, the proximal end of which is slightly applied to the posterior edge of the neural spine. In the adult, these two elements completely fuse to form an epural. A neural arch is present on the last centrum.

The caudal fin of *Box* is therefore homocercal, and slightly more specialized than that of *Cantharus*, on account of the fewer hypurals to the last vertebral segment.

*SMARIS ALCEDO.* (Perciformes, Mænidae.)

A fairly long and free urostyle is present, on the ventral side of which, together with the last centrum, are four fin-ray supports, three only of which are undoubted hypural bones; the last is somewhat doubtful. Both the penultimate and antepenultimate vertebrae bear hypurals, between the distal ends of which is a large cartilage bearing small fin-rays. Separated from this cartilage only by the distal end of the first hypural are two small cartilages, both of which support the very small anterior epaxial fin-rays; a similar cartilage dorsally performs the same function. Three definite dorsal caudal radials are present and one epural bone; neural arches are borne by each of the last two vertebrae. A splint-like bone is closely fitted between the distal ends of the urostyle and the neural arch of the last centrum; probably it is a neural arch itself, belonging to some vertebra now absorbed into the urostyle. Cartilaginous epiphyses are present on most

of the fin-ray supports, and here and there are additional distal cartilages applied to these epiphyyses; they may represent the persistent distal segments of radials.

This caudal fin is a good intermediate form between the lowly and the highly specialized homocercal types.

*LABRUS FESTIVUS.* (Perciformes, Labridæ.) (Plate XLIX. fig. 21.)

No urostyle can be seen in this form, it having completely fused with the last hypural bone; thus the last hypural, urostyle, and last centrum (*l.v.*) become a single bone. The last centrum bears one other hypural similar in size to the last; the preceding centrum also bears a hypural bone. Between the hypural of the penultimate vertebra and the first of the last centrum is a large bone (*v.c.r.*), which on account of its not having actually fused with the centrum, is probably better referred to as a ventral caudal radial. Three bony dorsal caudal radials (*d.c.r.*) are situated between the neural arch of the antepenultimate vertebra and the last hypural bone. In an exactly corresponding position dorsally and ventrally (*i. e.* on either side of the distal end of the neural spine and hæmal spine of the antepenultimate vertebra) are two cartilages (*c.*) the posterior of which may in some species, e. g. *Labrus turdus*, become quite radial-like. The extremity of the spinal cord is protected along the dorsal side of the last hypural by a secondary bony development (*s.*).

Though the structure of this caudal fin approaches closely to secondary symmetry as regards general form, it is really not symmetrical owing to the fact that by far the majority of dermatrichia are hypaxial. By the loss of the urostyle and the reduction of the number of hypurals to the last vertebral segment to two, this caudal fin is a considerable advance in homocercy on the preceding type.

*SCOMBER SCOMBER.* (Scombriformes, Scombridæ.) (Plate XLIX. fig. 22)

The tail of the Mackerel is somewhat difficult to interpret at first sight as regards the ending of the vertebral axis; it appears as though a well-marked urostyle were present extending to the length of the broad hypural bones. Examined more closely, doubts will arise as to its true urostylar nature for one or two reasons:—(1) its end is cartilaginous and it bears dermatrichia; (2) its distal end is cut square, a feature no urostyle elsewhere possesses; (3) the end of the spinal cord enters slightly into the tissue of the proximal end of the bone. Another feature worth notice is that clearing agents do not reveal any indications of a normal urostyle fused with any other bone, and moreover, the conical last centrum does not turn upwards as a hook or reduced urostyle as so many other forms show, but ends in a direct straight line. The tail of *Trachinus* is the only other one examined which closely resembles *Scomber* in the termination of

the axis, and clearing agents show, in this type, an oblique line of fusion in the proximal end of this rectangular bone; this suggests that the distal end is hypural, and the proximal, at least partly, is urostyle firmly fused with the hypural. It may be so in *Scorpaenidae* too, but the fact that the spinal cord enters the proximal end suggests that a neural arch is also involved. And this seems to be the interpretation, for it cannot be urostyle alone, since it is cut square, tipped with cartilage and bears dermatrichia just as an ordinary hypural does. It seems safe, therefore, to say that the urostyle is greatly reduced and fused entirely with the last hypural—in this case a small one. In all, then, four hypurals are associated with the last vertebral segment; the most anterior being provided with a ridge for the attachment of muscles. Two dorsal caudal radials are present. The penultimate vertebra possesses a reduced neural arch and a well-developed hypural, while the antepenultimate vertebra bears an epural and a hypural bone. All the hypurals are firmly attached proximally; the dermatrichia embrace the terminal endoskeletal supports to their base; thus the fin forms a most efficient organ of locomotion, seen to advantage in the swift swimming Mackerel.

*ZEUS FABER.* (Zeorhombi, Zeidae.) (Plate XLIX. fig. 23.)

In this fish, the John Dory, a fairly typical flat-fish form is met with. The urostyle is lost to view; clearing shows it to be present as a minute hook embedded in the tissue of the last hypural. The three terminal hypurals (*hy.*) are fused with the last centrum (*l.c.*) into a single piece, though the outlines of the hypurals still remain visible. The last two complete centra each have a well-developed epural (*ep.*) and hypural bone, and the former are specially interesting inasmuch as they show clearly that the epural is formed by a fusion of radial with neural spine, apparently by means of a secondary ossification. The last centrum has a small neural arch (*n.a.*) developed. Of other supports of dermatrichia there are two dorsal caudal radials (*d.c.r.*) between the last epural and hypural, and also a ventral caudal radial (*v.c.r.*) immediately anterior to the large terminal hypural plate. The caudal fin, therefore, is a specialized homocercal type.

*SOLEA LUTEA.* (Zeorhombi, Pleuronectidae.) (Plate XLIX. fig. 24.)

*Solea lutea* may be taken as possessing a good representative type of Pleuronectid caudal fin. It has a more delicate build, but essentially is very similar to that of *Zeus*. A clearing agent shows the otherwise invisible urostyle to be a mere hook-like upwardly directed termination of the last centrum. The four hypurals of this centrum are firmly united, though less so than in *Zeus*, and occupy a terminal position. The penultimate vertebra has a well-developed epural (*ep.*) and hypural (*hy.*) bone; since reference has been made by Cole to the corresponding epural and hypural in the Plaice, it is interesting to compare them in the

two species. In the Liverpool Biological Committee Memoir on the Plaice, Cole says, on p. 50:—"In the last distinct vertebra (*i. e.* the penultimate vertebra) it will be seen that the neural spine resembles the haemal spine in structure, but that both are peculiar. Each consists of a partly cartilaginous shaft behind and a thin laminate portion in front. The posterior shafts so closely resemble the succeeding epural (*i. e.* dorsal caudal radial) and hypural (*i. e.* ventral caudal radial) bones respectively *as to suggest that an epural above and a hypural below have fused on to the laminate portions*, which latter are undoubtedly similar to and perhaps represent the neural and haemal spines in front. As, however, we have no positive evidence of such a fusion, the spines in question are here described as simple neural and haemal spines." Though in *Solea lutea* this point is not so obvious as in *Pleuronectes*, there is to be seen a distinct fusion line running transversely across the proximal part of the epural, so that a parallelism does occur between the two species. I take it that Cole reserves committance on the subject on the ground that actual fusion has not been observed during development; but it is scarcely to be expected that such a minute feature as the fusion of a radial with a neural or haemal spine will be recapitulated in development, so that lack of embryological evidence would not be fatal to the theory. But we have seen in the case of *Bonaparte* that such a fusion can be traced in development; had Cole been acquainted with this as well as numerous other examples resembling that of the Plaice, he doubtless would have considered these epurals and hypurals more than mere neural and haemal spines.

To complete the description of the caudal fin of *Solea*, there are two dorsal caudal radials (*d.c.r.*) between the epural and hypural bones; in the corresponding position ventrally there is a ventral caudal radial (*v.c.r.*). The last centrum bears a neural arch (*n.a.*) which is not, as may be at first supposed, a urostyle, since the spinal cord (*sp.c.*) passes through it, in the fashion of other neural arches, in its course along the dorsal edge of the last hypural.

The caudal fin, then, is a homocercal type of an advanced nature. It may be mentioned that other species of *Solea*, *e. g.* *S. monochir* and *S. impar*, differ from *S. lutea* only in the number of terminal hypurals and the extent of their collateral fusion.

GobiUS PAGANELLUS. (Gobiiformes, Gobiidae.) (Plate L. fig. 25.)

The urostyle (*ur.*) is greatly reduced, and almost non-existent and fused with the last hypural bone. There are three hypurals, the last two, the largest, being fused to the last vertebral segment. A small trace of neural arch is present on the last centrum and that of the penultimate is also reduced. Dorsally there are two caudal radials (*d.c.r.*) and ventrally one (*v.c.r.*); the latter lying between the first and second hypurals. The spinal

cord can be seen to extend along the whole length of the last hypural.

Cartilage enters very considerably into this caudal fin. Both the anterior dorsal and anterior ventral fin rays are supported by cartilage which is somewhat irregularly disposed, and which extends inwards even to the vertebral axis. It is the irregular nature of these cartilages that has led me to attach no importance to them as homologues of ordinary supporting elements such as radials, but merely to regard them, both here and frequently elsewhere, as convenient secondary developments to support the less important dermotrichia.

I have been fortunate in obtaining a fairly good series of developmental stages of *Gobius*, and the larvae show exceedingly well how a condition in which the urostyle is very much reduced in the adult, is preceded by stages in which this structure is very prominent; and how, by a secondary encroachment of the last hypural bone, the urostyle is incorporated with this hypural.

The caudal fin of *Gobius paganellus* is a type of considerably advanced homocercy.

#### ECHENEIS NAUCRATES. (Discocephali.)

A long well-developed urostyle is present, attached to which, together with the last centrum, are six hypural bones closely fitting together. A well-developed neural arch is closely applied to the dorsal edge of the last vertebral segment; the penultimate vertebra possesses a hypural and an epural, and immediately posterior to the latter are three dorsal caudal radials, slenderly built. This fin must therefore be considered a lowly specialized homocercal caudal.

#### SCORPÆNA SCROFA. (Scleroparei, Scorpenidae.) (Plate L. fig. 27.)

The vertebral axis ends in a well-marked and free urostyle. Three undoubted hypural bones are attached to the last vertebral segment, while in a direct line with the axis of the urostyle is a slender ray-bearing bone which may be considered a hypural or a radial. Between this bone and the epural (*ep.*) attached to the antepenultimate vertebra are three dorsal caudal radials (*d.c.r.*). The neural arch of the penultimate vertebra is reduced; there is also a slender bone (*n.a.*<sup>1</sup>) immediately above, and closely approximated to the urostyle, which protects the delicate ending of the spinal cord; it is probably, therefore, a neural arch of some vertebra now absorbed into the urostyle. Both the second and third last vertebrae bear a strong hypural bone. This caudal fin is an excellent example of a form intermediate between a lowly and a highly specialized type.

#### TRIGLA LINEATA. (Scleroparei, Triglidae.) (Plate L. fig. 28.)

The urostyle here is practically non-existent, and traces of it can be seen only after the tail has been treated with a clearing

agent; thus the last vertebral segment and the last hypural become one solid structure. Three more hypurals are attached to the last vertebral segment and one is also attached to the preceding centrum. The whole of the dorsal contribution to the caudal fin is supported by four caudal radials. The neural arch to the penultimate centrum is much reduced. Though classified in the same division of Acanthopterygii as *Scorpena*, *Trigla* provides a striking contrast to this form in the degree of specialization of the caudal fin, being quite a highly specialized type.

URANOSCOPUS SCABER. (Jugulares, Trachinidae.)

The urostyle is absent or indistinguishably fused with the last hypural bone. Hypaxially, the last centrum bears three hypural bones, and epaxially a well-developed neural arch. The penultimate vertebra possesses a hypural bone, but its neural arch is greatly reduced; the antepenultimate vertebra bears both a hypural and epural. Between the epural bone and the neural arch of the last centrum are three dorsal caudal radials, while between this same neural arch and the hypural which is fused with the last centrum is a ray-bearing bone which is probably an epaxial element, though situated ventral to the spinal cord, since it is usual for the urostyle to fuse with the last, if any, of the hypural bones. This caudal fin, therefore, attains to a fairly high standard of homocercy.

CALLIONYMUS LYRA. (Jugulares, Callionymidae.) (Plate L. fig. 26.)

The caudal fin of *Callionymus* is a very simple type. No urostyle is present; the last vertebral segment has three hypurals firmly attached to it and to each other, thus forming a single piece, to which dorsally is also fused the neural arch of the last vertebra. The penultimate vertebra bears an epural (*ep.*) and a hypural, and one dorsal caudal radial (*d.c.r.*) is present.

CRISTICEPS ARGENTATUS. (Jugulares, Blenniidae.) (Plate L. fig. 29.)

The urostyle is present only as a small hook embedded in the tissue of the last hypural bone. Hypaxially, the last vertebral segment possesses two hypurals of about equal size, while dorsally it shows traces of two neural arches, through which the spinal cord passes on its way some distance beyond the end of the axis. The penultimate vertebra possesses an epural and a hypural; posterior to this is a large dorsal caudal radial. Immediately adjoining the distal end of the last hypural, and on its dorsal side, is a small ray-bearing cartilage, and another one on either side of the dorsal radial. Similar cartilages are to be found ventrally in a corresponding position. This caudal fin, therefore, will be regarded as a highly specialized homocercal type.



OPHIDIUM BARBATUM. (Jugulares, Ophidiidae.) (Plate L. fig. 30.)

All the median fins of this fish are continuous with one another, and the caudal proper may in this particular case be limited to those dermatrichia which are not supported by the typical radial or somactid of the dorsal and anal fins. This confines the caudal rays to those eight or nine supported by a large terminal hypural, often deeply and irregularly cleft, which is firmly coalesced with the last vertebral segment; the urostyle therefore is reduced to the merest vestige. A diminished neural arch is to be seen on the last centrum, and the nerve-cord runs along the whole length of the dorsal edge of the hypural. Thus the caudal fin itself is exceedingly simple in form and very highly specialized. The neural and hæmal arches of the penultimate vertebra have a cartilaginous shaft fused to their posterior side; in reality, therefore, they may be considered epural and hypural respectively, but bearing no fin-rays.

*General remarks on the Acanthopterygian Caudal Fin.*

A sufficient number of types from various divisions of the Acanthopterygii have been dealt with to show how, in a single sub-order of Teleosts, the structure of the tail-fin may vary. Even in the same division of the sub-order, vastly different types are found; for example, in the Perciformes, the genera *Serranus*, *Box*, *Cantharus*, and others have features characteristic of the less specialized homocercal tail, such as a long and free urostyle and a large number of hypural bones attached to the last vertebral segment; on the other hand, the Wrasses (Labridæ) have lost these lowly specialized features and attained to the rank of high specialization. The Scleroparei provide a similar contrast, *Scorpena* having a much less advanced type than *Trigla*. It would be difficult to account for such variations between types otherwise so closely related, except on physiological grounds, but it indicates that the tail-fin is not a safe guide, or rather, a wholly satisfactory character, by which fishes can be classified.

In the main, however, advanced homocercy is exhibited among Acanthopterygian caudals, except for the Perciformes; this division possesses the greatest number of less specialized tails (the Labridæ are the only family with much exception), but it is, as a division, the least specialized among the Acanthopterygii. From the foregoing descriptions it will be seen that the Jugulares possess the most advanced types of homocercy; of the six genera which have been subjected to examination, viz. *Uranoscopus*, *Trachinus*, *Lepadogaster*, *Blennius*, *Cristiceps*, and *Ophidium*, all possess advanced features in the caudal fin; but the Jugulares are, as a division, among the most specialized of the Acanthopterygii. The Zeorhombi occupy an intermediate position, and all members have very similar tails: they have a greatly reduced urostyle fused with a hypural, and also a large number of hypurals to the

last vertebral segment; thus there is an advanced feature (the former) and a lower feature (the latter) both present in the same caudal—in other words, an intermediate condition in specialization is present, which is consistent with the intermediate position the division occupies among the Acanthopterygii.

It would, therefore, seem that each individual division has its own grades of specialization within itself, and in this minor classification the structure of the tail does correspond with the general structure of the fish in respect to specialized features in general. In the Perciformes, the Serranidae are among the least specialized of the several families, and the Labridae are at the other end of the scale; and it has been pointed out that members of the former family have less specialized tails, by far, than those of the latter; thus caudal features correspond with specialized features in general, within this division. Exactly the same thing occurs among the Scleroparei, where the least specialized members are the Scorpaenidae and one of the most specialized the Triglidae; the Scorpaenidae have lowly and the Triglidae highly specialized caudal fins.

The Scleroparei are a more specialized division than the Perciformes, and yet *Scorpena*, among the former, has a less specialized tail than that of *Labrus* in the latter division. Thus while the caudal fin may not be depended upon as a feature for classification in a broad sense, it may be useful within the scope of a single division.

#### OPISTHOMI.

##### MASTACEMBELUS sp. ? (Plate L. fig. 31.)

This fish possesses a continuous undifferentiated median fin; the urostyle is well-marked and free, and equal in length to a vertebra. The limits of the caudal fin proper are probably best fixed here by those dermotrichia supported by hypural bones, of which two are associated with the last vertebral segment, the anterior one being obviously composed of three fused collaterally, and one with the penultimate vertebra. All the remaining fin-rays of the median fin are borne by radials; no epurals are present. A trace remains of the neural arch to the last vertebra. Thus the tail is definitely homocercal; in regard to this, it is strange that authors refer to it as a gephyrocercal tail. The only possible foundation for so naming this type is the apparent symmetry due to the confluent fins; it must, however, be insisted on that gephyrocercy indicates true secondary symmetry, *i. e.* an abbreviated protocercal condition. It is obvious that such a tail as that of *Mastacembelus* cannot be referred to the same category as that of *Fierasfer*.

#### PEDICULATI.

##### LOPHIUS PISCATORIUS. (Plate L. fig. 32.)

This fish may be said to illustrate the extremest type of advanced homocercy. Practically only one hypural is present,

though this is somewhat cleft distally; this structure is the sole support of the eight caudal rays; the last vertebral segment has become most completely fused with the hypural. The whole fin presents a most compact and solid structure. The neural and haemal spines form an imbricate series, each overlapping the one behind.

#### PLECTOGNATHI.

*BALISTES CAPRISCUS.* (Sclerodermi.) (Plate L. fig. 33.)

No trace of a urostyle remains, and two large hypural bones are firmly united with the last centrum. For such an advanced condition of homocercy an irregularity occurs here, for the penultimate vertebra possesses an epural bone (*ep.*) instead of the usually greatly reduced neural arch; the penultimate vertebra also bears a hypural bone. Two dorsal caudal radials (*d.c.r.*) are closely wedged between the epural and last hypural, and a ventral caudal radial (*v.c.r.*) is found between the first and second hypural. The whole fin presents an apparent symmetry.

#### 4. GENERAL CONCLUSIONS.

There is every reason for believing that the most specialized caudal fins have been evolved from a common primitive type, which is referred to as protocercal; modifications of this produced the heterocercal form, which in turn was followed by the homocercal type.

**PROTOCERCY.**—A protocercal fin may be defined as one which is primitively symmetrical externally and internally, and hence one which has not undergone any reduction or modification of the original form. It is very probable that the protocercal tail is not found in the adult condition among any living fishes. The Cyclostomes are sometimes credited with having a protocercal caudal, but it may be that it is a degenerate condition, and not a persistent original structure. Since the original protocercal caudal fin was continuous with the dorsal and anal fins, and thus undifferentiated, it is not unreasonable to suppose that the continuous fin was supported similarly throughout, *i. e.* by a series of radials.

It must not be supposed, however, that protocercy is always associated with a continuous median fin; during development in Teleosts the elements of the permanent differentiated median fins are laid down before heterocercy is established, so that there is evidence for supposing that differentiation of the median fins occurred in adult forms before heterocercy was adopted.

**HETEROCERCY.**—Confining attention to typical forms, the heterocercal caudal fin may be defined as one in which the extremity of the chorda is directed upwards, and which as a consequence is unsymmetrical, the lower lobe being larger than the upper, and, moreover, one in which, when centra are formed, these elements remain distinct to the end of the axis.

Reference to fig. 1 (Pl. XLVII.) will render a full description unnecessary; this form may be considered quite typical except in possessing what may be regarded as an incipient urostyle at the extreme end of the axis. It should be observed that on the dorsal side the separation of the radials from the neural arches anteriorly, and their gradual approach to and ultimate fusion with them posteriorly, suggests that when the median fins were continuous there was a gradual transition, from before backwards, from widely separated radials to fusion of radials and arches. There is evidence that the same thing occurred ventrally, but the fusion of radials and arches has taken place much further forward owing to the fact that the enlarged lobe required a much firmer base of support; several Elassmobranchs retain the line of fusion in the adult (e. g. *Galeus* and *Acanthias*).

**HOMOCERCY.**—The homocercal type of caudal fin is characteristic of the Teleostei, and is a specialized form of heterocercy. Though the term is very broad in application, a tail-fin which is externally symmetrical, but in which the majority of the fin-rays are supported internally by hypaxial elements, and in which a true urostyle is present either in the adult or some time during larval history, may safely be referred to as a homocercal caudal fin.

Special attention has been directed towards ascertaining which features may be used to determine the degree of specialization exhibited by the homocercal caudal fin; these characters may be enumerated as follows:—

I. *Characters indicative of a low degree of specialization:—*

- (a) Notochord exerted beyond the actual vertebral axis.
- (b) Long urostyle, not incorporated with an adjacent hypural bone.
- (c) Vestiges of fin-ray supports of the nature of opisthural cartilages.
- (d) Large number of hypural bones associated with the last vertebral segment.

*Clupea* may be quoted as an example of this type.

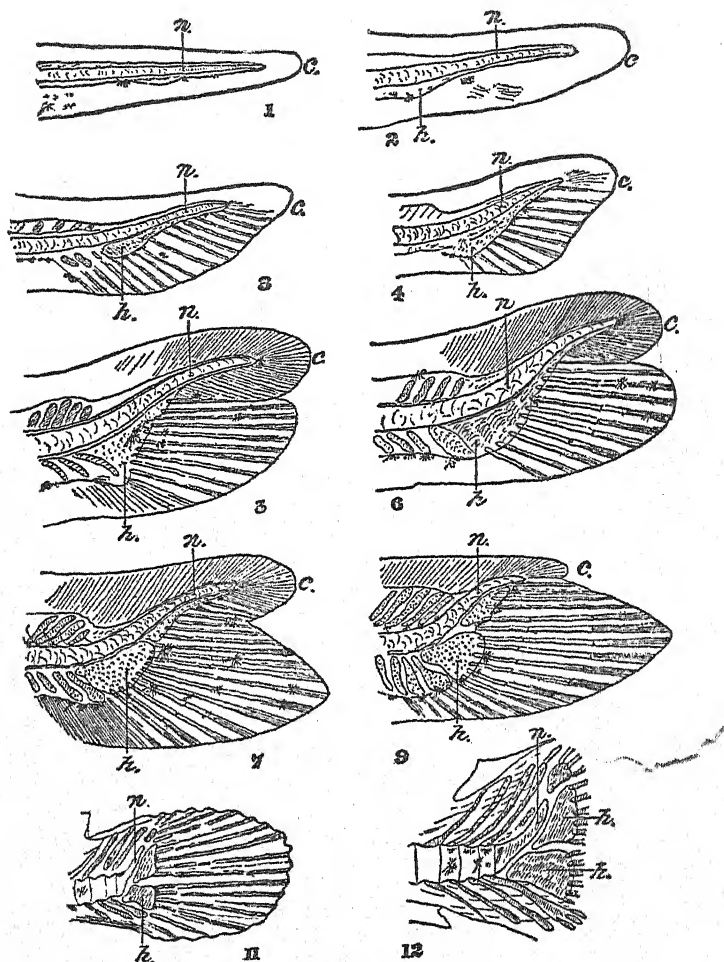
II. *Characters indicative of a high degree of specialization:—*

- (a) Greatly reduced urostyle, fused with a hypural bone.
- (b) Reduction of the number of hypurals associated with the last vertebral segment.

Among the caudal fins examined there is considerable evidence forthcoming to substantiate the view that hypurals and epurals are formed by the fusion of vertebral arches and radials, and the following may be quoted as affording examples:—*Acanthias*, *Galeus*, *Heterodontus*, *Acipenser*, *Polyodon*, *Synodontis*, *Plotosus*, *Anguilla*, *Conger*, *Gadus*, *Gadiculus*, *Molva*, *Motella*, *Centriscus*, *Belone*, *Box*, *Zeus*, *Pleuronectes*.

The figures here reproduced from those of Agassiz are interesting in showing how, in homocercal tails, the original caudal fin is replaced by a more anterior fin; I have observed exactly the same thing in *Atherina*, and it is highly probable that it is quite

Text-fig. 57.



Development of the tail of the Flounder. After Prof. Alex. Agassiz.  
*n*, notochord; *c*, embryonic caudal fin; *h*, hypural plates.

a general rule. The deep incision between the original and permanent caudal is very probably only the vestige of a once prominent gap between the two fins, and hence the homocercal

caudal fin may be considered to be a posterior anal—or, in other words, a more anterior part of the ventral median fin—brought into a terminal position by the great abbreviation and upturning of the chordal axis.

GEPHYROCERCY.—A gephyrocercal caudal fin may be defined as one which is quite symmetrical, externally and internally, but with symmetry secondarily acquired. *Pteraspis dentatus* may be quoted as a typical example. Many forms which are generally considered gephyrocercal (e. g. *Mastacembelus* and *Anguilla*) are not so, but clearly homocercal. It is worth noticing that there is no embryological evidence that heterocercy preceded the gephyrocercal condition.

Many other terms are used in works dealing with the caudal fin, but the four terms here used—protocercal, heterocercal, homocercal, and gephyrocercal, understood as defined here—will probably include any type of piscine caudal fin. A common term not insisted on in the present paper is diphyccercy, which implies perfect symmetry, externally and internally; it tends to be ambiguous, for symmetry may be either primitive or secondary, and primitive diphyccercy corresponds to protocercy, while secondary diphyccercy corresponds to gephyrocercy. However, diphyccercy may sometimes prove useful to apply to a truly symmetrical fin about which any doubt may exist as to its primitive or secondary nature.

TAXONOMIC IMPORTANCE.—The structure of the caudal fin cannot be considered a safe criterion for taxonomic purposes, though it may be useful in this connection among the smaller divisions, as is well illustrated by the Acanthopterygii.

## 5. ADDITIONAL NOTE.

Since the foregoing paper was written, Professor Dollo has drawn my attention to his memoir on the fishes of the 'Belgica' Expedition of 1897-99 (see Literature, ref. 11), where he advocates a double nomenclature for the caudal fin. Briefly, this author considers it necessary to adopt two terms—(1) physiological, and (2) morphological. This may be conveniently summarized as follows:—

I. PHYSIOLOGICAL (or ETHOLOGICAL), which refers to the external form of the fin in its relation to the mode of life.

- (1) *Rhipidocercal*, implying an expanded or fan-shaped form.
- (2) *Gephyrocercal*, implying a tapering form.

II. MORPHOLOGICAL, which refers to the internal structure of the fin.

- (1) *Diphyccercal* (or *Protocercal*).
- (2) *Heterocercal*.
- (3) *Homocercal*.

As a result of some discussion on the subject, Professor Dollo and myself are of the opinion that the following modification is advisable :—

I. **PHYSIOLOGICAL**, which refers to external form.

- (1) *Rhipidocercal*, implying an expanded or fan-shaped form.
- (2) *Oxycercal*, implying a tapering form.

II. **MORPHOLOGICAL**, which refers to internal structure.

- (1) *Protocercal*.
- (2) *Heterocercal*.
- (3) *Homocercal*.
- (4) *Gephyrocercal*.

For the use of those who prefer to adopt this double nomenclature, a few illustrations may be found useful.

Rhipidocercal homocercal .....	<i>Polyodon</i> .
Rhipidocercal gephyrocercal ...	<i>Orthogoriscus</i> .
Oxycercal heterocercal .....	<i>Chlamydoselachus</i> .
Oxycercal homocercal .....	<i>Anguilla</i> , <i>Mastacembelus</i> .
Oxycercal gephyrocercal .....	<i>Pieraster</i> .

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\* It was not until the manuscript was ready for the press that my attention was drawn to this excellent work.

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B.D.	.....	Basi-dorsal.
c.	.....	Cartilage supporting fin-rays.
d.	.....	Distal segment of radial.
d.c.r.	.....	Dorsal caudal radial.
der.	.....	Dermotrichia.
e.b.	.....	Ensheatheing bone protecting notochord.
ep.	.....	Épural.
f.	.....	Fulera.
h.	.....	Hvatus between dorsal and ventral rays.
h.a.	.....	Hæmal arch.
h.p.	.....	Hypural.
I.D.	.....	Inter-dorsal.
l.v.	.....	Last vertebra or centrum.
m.	.....	Median segment of radial.
n.	.....	Notochord.
n.a.	.....	Neural arch.
n.a. <sup>1</sup>	.....	Probably a neural arch protecting end of spinal cord.
n.s.	.....	Neural spine.
o.c.	.....	Opisthural cartilage.
p.	.....	Proximal segment of radial.
p.v.	.....	Penultimate vertebra or centrum.
s.	.....	Secondarily developed bony sheath protecting the spinal cord.
sp.c.	.....	Spinal cord.
ur.	.....	Urostyle.
v.c.r.	.....	Ventral caudal radial.

## EXPLANATION OF THE PLATES.

## PLATE XLVII.

Fig. 1. Caudal fin of *Heterodontus philippi*. Illustrating a typical Elasmobranch heterocercal caudal fin. At the anterior end of the ventral lobe will be seen two radials (v.c.r.) quite distinct from the hæmal arches. Dorsally, at the anterior end of the fin, the radials are well separated from the neural arches. The proximal ends of the horny fibres have, throughout the fin, been removed in order to expose the endoskeletal supports.



- Fig. 2. Caudal fin of *Acipenser sturio*. Illustrating the Ganoid heterocercal form. The proximal ends of the fulera and dermatrichia have been cut away to expose the endoskeletal supports.
3. Caudal fin of *Polyodon spatula*. Illustrating a more specialized heterocercal Ganoid caudal. As in the preceding types, the proximal ends of the dermatrichia and fulera have been removed.
4. Caudal fin of *Ania catra*. Modified from K  lliker. Illustrating a highly specialized heterocercal form: usually referred to as hemi-heterocercal.
5. Caudal fin of *Clupea pilchardus*. Illustrating a lowly specialized homocercal caudal.
6. Caudal fin of *Notopterus borneensis*. On the ventral side the caudal is continuous with the anal fin.
7. Caudal fin of *Plotosus* sp.? Drawn from a young specimen 1½ inches (3.8 cm.) in length. The fin-rays (*der.*) on the dorsal side illustrate the "procurent caudal" of Regan. Note that the first fin-ray anterior to the hypural of the penultimate vertebra has no radial as a support, and thus seems to anticipate a similar condition ventrally as is found dorsally.
8. Caudal fin of *Synodontis schall*. The fusion of radials and arches clearly shown.

## PLATE XLVIII.

Fig. 9. Caudal fin of *Leptocephalus brevirostris*.

10. Caudal fin of *Anguilla vulgaris*, 4¼ inches (12 cm.) in length. Of the 10 rays which are truly caudal, 6 are bifurcated distally. Note the excellent evidence of fusion of radial with haemal spine shown in the first hypural, the fusion line being very distinct.
11. Caudal fin of *Anguilla vulgaris*, adult. The urostyle and last centrum have completely coalesced with the last hypural.
12. Caudal fin of *Conger vulgaris*. The figure was drawn from a specimen cleared in xylol, thus showing the outline of the last vertebra (*l.c.*), which otherwise remains invisible. The first and second hypurals show the fusion of radial and arch extremely well. The dermatrichia are cut short.
13. Caudal fin of *Myrus vulgaris*. Cleared in xylol.
14. Caudal fin of *Plecogaster (Echiodon) dentatus*. From Emery. Illustrates extreme condition of geophyrocerey. A distinct gap can be seen in the median line separating the dorsal and ventral dermatrichia.
15. Caudal fin of *Syngnathus acus*. Illustrates an extremely simple type of homocerey, very symmetrical in appearance, though really wholly hypaxial.

## PLATE XLIX.

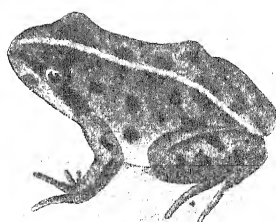
Fig. 16. Caudal fin of *Ammodytes tobianus*.

17. Caudal fin of *Mola vulgaris*. The dorsal caudal radials (*d.c.r.*) are quite free, but slightly overlap the neural arch of the penultimate vertebra, thus giving, in the figure, the appearance of fusion.
18. Caudal fin of *Gadiculus argentatus*. One of the best instances among Teleostei of the formation of hypurals and epurals by the coalescence of radials and arches; radials are to be seen in the various stages of fusion.
19. Caudal fin of *Serranus cabrilla*. A somewhat loosely constructed skeleton and a type of homocerey frequently met with among the Acanthopterygii.
20. Caudal fin of *Boia salpa*. Figured from a specimen 4 cm. long. The young stage has been chosen on account of the neural arch of the penultimate vertebra being separate from the dorsal caudal radial immediately posterior to it: these two elements fuse in the adult condition; otherwise the adult form is the same.
21. Caudal fin of *Labrus festinus*. The figure gives the appearance after clearing with xylol.
22. Caudal fin of *Scomber scomber*. Figured as seen after clearing agents were used; note the last centrum shows no sign of upturning at its posterior end.
23. Caudal fin of *Zeus faber*.
24. Caudal fin of *Solea lutea*. As it appears when cleared in xylol. Note the spinal cord pierces the neural arch of the last centrum.

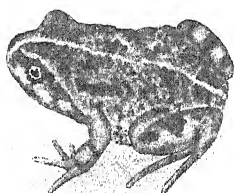




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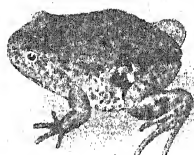
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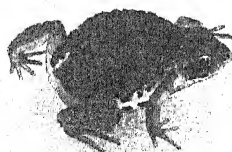
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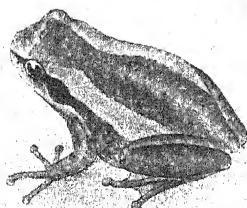
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TASMANIAN FROGS.

## PLATE L.

- Fig. 25. Caudal fin of *Gobius pagauellus*. Note the large amount of cartilage entering into the skeleton.
26. Caudal fin of *Callionymus lyra*. A very advanced form of homocercy with no complications.
27. Caudal fin of *Scorpena scrofa*. Intermediate between a lowly and a highly specialized homocercal caudal.
28. Caudal fin of *Trigla lineata*. Figure drawn from a cleared specimen, showing well the vestige of a urostyle.
29. Caudal fin of *Cristiceps argentatus*.
30. Caudal fin of *Ophidium barbatum*. The caudal proper is confined to the rays attached to the terminal hypural bone. Note the cartilaginous shaft fused to the posterior side of the neural and hæmal arches of the penultimate vertebra. The median fins form a continuous series.
31. Caudal fin of *Mastacembelus* sp.? Forms part of continuous median fin, but the caudal proper is wholly hypaxial.
32. Caudal fin of *Lophius piscatorius*. The extreme case of advanced homocercy—a totally hypaxial fin.
33. Caudal fin of *Balistes capricus*.

## 2. Some Notes on Tasmanian Frogs.

By T. M. SAVAGE ENGLISH\*.

[Received March 10, 1910.]

(Plate LI.†)

Taking into consideration its outlying position and its comparatively small size, Tasmania is the home of a surprisingly large number of frogs.

Seven species have come under my own observation, and it is about these that the following notes were made in the years 1901-3. These species, all of which, I believe, are also found in the neighbouring State of Victoria, are:—

1. *Limnodynastes tasmaniensis*.
2. *Limnodynastes dorsalis*.
3. *Crinia signifera*.
4. *Crinia lævis*.
5. *Pseudophryne bibronii*.
6. *Hyla ewingii*.
7. *Hyla aurea*.

No others than these seven have come under the notice of Mr. J. J. Fletcher (Proceedings of the Linnean Society of N. S. W. 1897, p. 662). He and others, including myself, have tried in vain to find *Crinia tasmaniensis*, and Mr. Boulenger considers that, though this is beyond doubt a well-marked species, there is reason for thinking that the specimens of it which have belonged to the British Museum since 1858 may not have come from Tasmania.

\* Communicated by G. A. BOULENGER, F.R.S., V.P.Z.S.

† For explanation of the Plate see p. 634.

Two other frogs, *Limnodynastes peronii* and *Hyla peronii*, have been credited to Tasmania, in both cases on the strength of single specimens presented to the British Museum by Sir A. Smith before 1858. Here, again, the evidence of locality seems doubtful. But in a mountainous and forest-clad country, frogs, however abundant they may be, are difficult to find, and it is only a small portion of Tasmania that has been explored for them at all; so that it is quite possible that these and perhaps other species may exist.

The Tasmanian climate is on the whole mild and even, with regular seasons. Its winter resembles that experienced in the south of Europe, though the mean temperature of summer is not higher in Tasmania than it is in the north of France. The rainfall is distributed over the year, and the droughts of the Australian mainland are unknown.

This climate allows the frogs of Tasmania to breed at almost any time; so that it is nearly always possible to find tadpoles in any suitable pond. But each species seems on the whole to keep to its own particular season.

Taking the species in order:—

1. *LIMNODYNASTES TASMANIENSIS*. (Plate LI. figs. 1, 2.)

I found this frog abundantly in the neighbourhood of Hobart in the south-east, and towards the north, around Launceston and Westbury. These places have a smaller rainfall than the average for the island. On the north-west coast, where, at Ulverstone and Devonport, there is sufficient rain for tree-ferns near sea-level, I did not find it.

The stone, or log, under which it makes its home during the day, is usually in a somewhat moist place, but *Limnodynastes tasmaniensis* is decidedly terrestrial in its habits. I never found a single individual in the water, and if thrown in it at once makes for the bank, swimming badly.

A well marked specimen of this frog is a really beautiful creature: light brown inclining to yellow, or occasionally pink, with large and regularly placed spots, which may be either rich dark brown or green, with or without a lighter edging. From this coloration it may vary to an almost uniform dark brown, sometimes looking almost black. The dorsal stripe is generally bright yellow.

I found one at Westbury, towards the end of summer (February 1902), whose dorsal stripe was of a brilliant orange, almost red (cf. colour variations of *Hyla ewingii* and *Crinia signifera* from the same place).

I was not able to determine satisfactorily the note of *Limnodynastes tasmaniensis*, though a noise like two stones being sharply struck together, which I repeatedly heard from a heap of loose rock on the bank of the North Esk, near Launceston, in April, 1901, must have come from either this species or *Hyla aurea*. Numbers of both were under the stones, but no other frogs.

2. *LIMNODYNASTES DORSALIS*. (Plate LI. fig. 3.)

Of this species, which is widely distributed over the mainland of Australia, and is probably common in most parts of Tasmania. I only secured one adult specimen. This I found at the end of a burrow in sand under a large stone. It was in a rather dry part of some Eucalyptus "bush," but not far from a small pond.

If I am right in supposing that a loud booming note, which can be heard considerably more than a quarter of a mile away, is due to this species, it is common in the neighbourhood of Hobart, Launceston, Fingal (in the east of the island), and on the north-west coast.

The only other frogs to which this note could be reasonably attributed would appear to be *Limnodynastes tasmaniensis* and *Hyla aurea*; but the former does not seem to occur on the north-west coast, and the latter is not found near Hobart.

This is by far the most noticeable frog-music in Tasmania, and when, as is usually the case, a number of frogs are uplifting their voices together, the effect is that of a somewhat barbaric banjo performance. These concerts take place in or around some fairly deep pond, and, however quietly one approaches, according to my own experience, invariably cease before it is possible to exactly mark down the performers. I have never been able to notice any disturbance in the water, and believe that the frogs must be singing at the entrances of their burrows, and that these are well concealed under roots, stones, &c.

This frog, on the north-west coast, retired for the winter of 1902 about the middle of April, and was in evidence again towards the end of August.

At Ulverstone it was spawning towards the end of October, the egg-masses resembling lumps of froth about 6 inches, or rather less, across. On the 7th of November some of these had fairly large tadpoles in and under them. These tadpoles were very dark in colour, with violet reflections.

Earlier in the year (September) I had found some very large tadpoles of this species (3 inches long), with hind legs just forming, and at the same time some quite small ones. On the 10th of November some of these were showing signs of front legs, and by December they had become frogs.

3. *CRINIA SIGNIFERA*. (Plate LI. figs. 4, 5.)

This active and variable little frog was very common wherever I went in Tasmania, and its cricket-like chirp was to be heard at almost any time of the year; so that it does not seem to hibernate. It is decidedly aquatic, diving to the bottom at the slightest alarm and remaining motionless.

No kind of water seems to come amiss to it, from a rapid mountain stream to a muddy puddle. As a rule, however, it prefers water which is fairly shallow, and so is often obliged to become terrestrial during the heat of summer, when all the

shallow pools are dry. At this time of the year these frogs are to be found, almost always singly, under stones and in cracks in the ground, into which their small size allows them to go deep enough to find a secure and comparatively moist retreat.

They chirp to each other incessantly, by day as well as in the evening, and though the note of a single one is comparatively weak the combined efforts of the numbers which gather together in any suitable place can be heard a long way off.

On land these frogs are as active as crickets, and exceedingly difficult to catch. In the water they swim well.

The colour of *Crinia signifera* is as a rule dark brown or grey, but it is most variable. The male is darker than the female and may be almost black all over, though he is generally lighter underneath. The under surface of the female is usually white, with or without dark spots. While breeding, the male seems always to have a black throat. There is sometimes a tendency to bright brown or orange markings; and in February, 1902, I found one of these frogs at Westbury which was of a fairly bright orange all over (*cf.* colour variations of *Limnodynastes tasmaniensis* and of *Hyla ewingii* from the same place). The young and also the tadpoles are intensely black.

In January, 1901, I found that most of these frogs at Hobart, and at Zeehan in the west of the island, had the backs of their thighs and their hinder parts blood-red, giving them a truly diabolical appearance. I did not, however, find any of them coloured in this way except on these two occasions.

This species has a continued chirp, hardly to be distinguished from that of the mole cricket, which is such a common Tasmanian insect, or from that of *Pseudophryne bibronii*.

*Crinia signifera* has its main spawning season during the autumn and winter months, from May to August. At this time of the year these frogs are not nearly so active as usual, though of course this may be owing to the colder weather.

The male clasps the female round the waist.

The eggs are in masses, spread over stones and weeds at the bottom of shallow water, and the tadpoles are exceedingly small, as are the young frogs. These, at first, are less than a quarter of an inch in length.

#### 4. *CRINIA LÆVIS*. (Plate LI. fig. 6.)

I found this species abundantly on the north-west coast; also, when I had got to know where to look for it, at Westbury and near Launceston. But as it seems to be not only nocturnal but silent, it is very possibly far more common than it appears to be.

All my specimens were under logs or stones lying on swampy or at all events fairly moist ground, but, in complete contrast to *Crinia signifera*, *Crinia lævis* appears to be altogether terrestrial, not even going into the water to spawn. Indeed, in life-history and habits these two frogs seem to have nothing in common, while *Crinia lævis* closely resembles *Pseudophryne bibronii*. It is

perhaps a little more active than this last, but still is by no means difficult to catch.

The colour of this species, in Northern Tasmania, does not seem to vary much. Above it is light grey, becoming paler or white underneath, where it is marbled with dark grey or black. The "concealed surface" at the groin is pink marbled with black. A breeding pair, near Devonport, had irregular brown blotches on their backs, while the throat of the larger of the two was dull yellow.

This frog may perhaps be responsible for some of the chirping which comes from the haunts of the smaller Tasmanian batrachians, but of this I was never able to assure myself.

Its breeding habits are peculiar. It does not deposit its eggs in water, but in a smooth-sided underground chamber, either hollowed out or adapted by the parent frogs.

On the 30th of March, 1902, one of these nests contained two frogs as well as a mass of eggs. (I never found more than two frogs of this species together: cf. *Pseudophryne bibronii*.) This mass, after being put into water, held together for about a week; then the eggs separated. The tadpoles began to free themselves on the 4th of May. Their colour during their earlier development was a rather pale brown, but before leaving the egg they became quite dark. There was no appearance whatever of external gills; and while in the eggs the tadpoles did not move at all.

##### 5. *PSEUDOPHRYNE BIBRONII*. (Plate LI. fig. 7.)

This little toad, the only known representative of the Bufonidae in Tasmania, seems to be widely distributed over the island, for, though I never saw one of them except in the autumn, when they gather together for breeding, it was abundant wherever I happened to be at this time of the year: at Hobart, near Launceston, and near Devonport, in March, April, and May, 1901, near this last place in March and April, 1902, and at Perth in March, 1903.

After rain at the end of March, 1901, they became abundant and noisy near Launceston. I found over thirty packed closely together under one log.

This species is slow in its movements, and walks rather than hops. In the water it seems perfectly helpless, and as, like *Crinia lavis*, it leaves the necessary water for its tadpoles to be provided by subsequent rain, and frequents dry hilly country, it is probably, except for a short time as a tadpole, altogether terrestrial.

In colour it is dark brown above, occasionally almost black; beneath it is marbled, black and white or grey; while those parts of its legs which are usually concealed, except when it is walking, are brilliant yellow and orange. There are indications of a yellow vertebral stripe.

The note of *Pseudophryne bibronii* is a chirp, which I could not distinguish from that of *Crinia signifera*. As is the case with this last frog, the number of singers generally makes up for any



individual want of power, and the resulting concert can be fairly called noisy.

The breeding habits of the present species are to a large extent those of *Crinia laevis*, except that it is more social. I always found large companies gathered together under logs and stones in places where, after rain, ponds would form. They do not seem to make nests like *Crinia laevis*, but deposit their eggs under any convenient stone. (I never found any eggs under a log, but this of course may have been accidental.) The eggs do not seem to adhere either to each other or to anything else.

On the 20th of April, 1901, I found a collection of these eggs, which I put into water. The tadpoles began to wriggle at once, and within twelve hours they were free and swimming about.

#### 6. *HYLA EWINGII*. (Plate LI. figs. 8, 9.)

This frog seems to be abundant in most parts of Tasmania. The only place from which I might have recorded it, and did not do so, is Zeehan, and I am almost certain that this is an accidental omission.

It is on the whole aquatic, seldom going far from water, and living very generally under stones or logs on the bank of some pond or stream. When disturbed, it dives in with all speed.

It does not seem to be really arboreal, though it may occasionally climb up ten feet or so from the ground. I have never heard its note coming from the top of a tall tree, as one hears that of the European *Hyla arborea*, though this may perhaps be accounted for by the very slight shelter from either sun or enemies that a frog would find among the leaves of any full-grown Tasmanian *Eucalyptus*.

Where plants are kept in pots on a veranda a colony of these frogs usually settles, and its members seem to appreciate regular watering as much as the plants do, generally greeting it with song.

Except when breeding, *Hyla ewingii* is inactive during the day. Its regular concerts begin towards sunset, though, as is the case with many other frogs, its voice is heard when rain is approaching, or at times when certain loud noises excite it—rapid hammering, for instance.

It does not seem to hibernate, but is sluggish in cold weather.

Its colour is almost invariably some shade of brown, closely resembling that of its immediate surroundings.

Mr. J. J. Fletcher has found that near the summit of Mount Kosciusko, in New South Wales, frogs of this species are bright green. He attributes this to the fact that at this altitude, though the days may be warm, the nights are almost always frosty; so that no insects are abroad then, and the frogs have to hunt for food by day among green vegetation.

In January, 1902, I found a specimen at Westbury which had some bright green patches on its back. The colour of these patches seemed fixed; at all events it did not vary with that of the rest

of the frog according to its surroundings (*cf.* colour variations of *Limnodynastes tasmaniensis* and *Crinia signifera* from the same place).

The note of this frog resembles that of *Hyla arborea*, but is not so loud.

*Hyla ewingii* has its regular breeding season in winter. In July, 1902, it was spawning at both Launceston and Devonport, in pools and ditches such as would be chosen by *Rana temporaria*. Its spawn is in masses, very like those of this last frog but smaller. The first tadpoles appeared at the end of July. They are very small, and at first quite black, becoming paler and silvery underneath as they develop.

During November the pools they frequent in a normal season are fast drying up, and the water which remains is packed with tadpoles. Early in December these pools are mostly dry, and the tadpoles have either become frogs or perished, the place where the last water stood being covered by a layer of their dried-up bodies.

#### 7. *HYLA AUREA*.

This, the largest and most conspicuous of the Tasmanian frogs, seems to be decidedly local. I saw or heard of it only in the country drained by the North and South Esk rivers, which unite at Launceston to form the tidal Tamar, and by the Mersey, which falls into the sea at Devonport. There is only a low watershed between these two basins. Wherever it is found it seems to be abundant: near Launceston, Perth, Longford, Westbury, Fingal, and Devonport; and as it is diurnal, it is not likely to be overlooked if present.

In its habits it resembles *Rana esculenta*, being essentially aquatic, and in summer liking to sit in the sun near the water, into which it dives with a splash when alarmed. It is a powerful swimmer; its usual custom of returning at once to the bank after having dived in, can be well accounted for by the fact that the rivers it frequents all contain large trout. This frog seems to be impatient of cold. In 1902, at Devonport, it disappeared after a few frosty nights at the end of March and the beginning of April, though the weather was on the whole warm for quite six weeks after this. Near Launceston I found large numbers of these frogs under stones during April, 1901. I only once found one climbing; it had got about three feet from the ground in a bush.

A well-marked specimen of this species is most gorgeously coloured: green, gold, blue, and white; but from this it may vary to dull brown, and when about to retire for the winter to almost black.

Beyond an occasional and not very loud croak, I was never able to identify this frog's note, though for a considerable part of one summer my window overlooked a pond full of them.

I was not at any of the places which they frequent during their breeding-season: this is probably September or the beginning of

October. At Westbury, towards the end of January, 1902, tadpoles of this species were very abundant and were developing their hind legs. During February they became frogs.

These tadpoles are very fish-like in colour: greenish olive above, silvery white beneath. They make a most attractive spinning bait for large trout.

*Hyla aurea* is one of the many additions which have been made of late years to the fauna of New Zealand and to that of New Caledonia.

#### EXPLANATION OF PLATE LI.

Figs. 1 & 2. *Limnodynastes tasmaniensis*, showing different types of colouring.

Fig. 3. *Limnodynastes dorsalis*.

4. *Crinia signifera*, ♀ in the breeding season.

5. *Crinia signifera*, in late summer.

6. *Crinia lavis*.

7. *Pseudophryne bibronii*, with eggs showing the development of the tadpole.

8. *Hyla ewingii*, showing its normal colour.

9. *Hyla ewingii*, from a quarry of brightly coloured sandstone.

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April 19, 1910.

Dr. S. F. HARMER, M.A., F.R.S., Vice-President,  
in the Chair.

The Secretary read the following report on the additions made to the Society's Menagerie during the month of March 1910:—

The number of registered additions to the Society's Menagerie during the month of March last was 100. Of these 30 were acquired by presentation, 18 by purchase, 35 were received on deposit, 12 in exchange, and 5 were born in the Gardens.

The number of departures during the same period, by deaths and removals, was 190.

Amongst the additions special attention may be directed to:—

One Puma (*Felis concolor*) ♂, from Tucuman, presented by Alec S. Waley, Esq., on March 22nd.

Two Musquash (*Fiber zibethicus*), from North America, purchased on March 16th.

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#### *A new Monkey from the Malay Peninsula* \*.

On behalf of Mr. Oldfield Thomas, F.R.S., F.Z.S., two specimens were exhibited of a new Monkey of the genus *Presbytis*, which had been obtained by Mr. H. C. Robinson during a recent expedition to the northern parts of the Malay States.

\* Published by permission of the Trustees of the British Museum.

It was proposed to be called

*PRESBYTIS ROBINSONI* THOS.\*

Abstract P. Z. S. 1910, p. 25 (April 26).

A white Monkey, with darker underside, hands, and feet. General colour above creamy white; the hairs white to their bases, mixed, however, with a small number of blackish hairs. These dark hairs became more numerous on the sides and belly, where they outnumbered the white ones; the general tone of the under surface grey, about grey no. 6 or 7 on the belly, darkening to no. 5 on the throat and sides of neck. Outer side of arms to wrists whitish like back, inner side and whole of legs with an equal mixture of dark and light hairs, resulting in about grey no. 9. Hands and feet greyish brown, with a tinge of bistre in it. Tail greyish white throughout.

Skin of face dark, except the lips, which were white. Long hairs of occiput directed forwards. Hairs of forehead radiating from points over the temples with a median crest between them, but both the whorls and crests differed considerably in the two specimens. Ear-tufts white, considerably surpassed by the long brownish hairs which grew from the lower parts of the cheeks.

A female specimen was whiter throughout, the under surface more nearly whitish, but still darker than the upper surface.

Dimensions of the type, measured in the flesh:—

Head and body 565 mm.; tail 824; hind foot 177; ear 30.

*Hab.* Ko-Khau, Trang, Northern Malay Peninsula.

*Type.* Adult male. British Museum, No. 10.10.1.1. No. 1236/10 of the Selangor Museum Register. Original number 3184. Obtained for Mr. Robinson by a native collector, 10 January, 1910.

This fine Monkey, which was obviously not an albino, differed conspicuously from all its allies by its white upper and darker lower surface, all other members of the group having the belly lighter than the back.

Mr. Thomas had great pleasure in naming it after its discoverer Mr. H. C. Robinson, Director of Museums, Federated Malay States, by whose scientific energy our knowledge of Malay Mammalia had been so largely increased.

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*A Collection of small Mammals from China†.*

On behalf of Mr. Oldfield Thomas, F.R.S., F.Z.S., a collection of small mammals obtained by Mr. Malcolm Anderson in Southern Shen-si for the Duke of Bedford's exploration of Eastern Asia was exhibited. Observations were made on the value of this further contribution by the Society's President to the National Collection

\* The complete account of this new species appears here, but the name and a preliminary diagnosis were published in the 'Abstract,' No. 88, 1910.—EDITOR.

† Published by permission of the Trustees of the British Museum.

and on the resultant increase in our knowledge of geographical zoology, a subject in whose study the Zoological Society had always had so large a share.

A complete list of the specimens would be given later, but in the meantime Mr. Thomas gave the following account of the new forms\* :—

MYOTIS MYOSOTIS ANCILLA Thos.

Abstract P. Z. S. 1910, p. 25 (April 26).

Smaller, with shorter ears, and more drab-coloured than in true *myosotis*.

Size rather smaller than in *myosotis*, not so small as in *blythi*. Ears decidedly smaller than in *myosotis*. General colour above nearly approaching "drab" of Ridgway, very different from the "wood-brown" of *myosotis* and its pale Persian subspecies *omari*. Head rather greyer. Dark shoulder-patches more strongly defined than in *myosotis*, blackish brown. Under surface as in *myosotis*.

Skull slightly smaller than in *myosotis*, and the bullæ smaller in correlation with the shorter ears. Protocone apparently as in *myosotis*, not as described by Miller in *blythi* †.

Dimensions of the type, the starred measurements taken in the flesh :—

Forearm 61 mm. (range 59 to 62).

Head and body \*75 mm.; tail \*56; hind foot \*12; ear \*21.

Skull: greatest length 22.2, basi-sinual length 17, front of canine to back of *m*<sup>3</sup> 9.2.

*Hab.* Shang-chou, S.E. Shen-si. Alt. 3300'.

*Type.* Adult male. B.M. No. 10.5.2.4. Original number 2082. Collected 27 November, 1909.

This is the eastern representative of the common European *M. myosotis*. What its relationship is to the Indian form *blythi* remains to be seen when better specimens of the latter are available for examination. But the type of *M. blythi*, received in the British Museum in the Tomes collection, is decidedly smaller.

MICROTUS (EOTHEXOMYS) NUX Thos.

Abstract P. Z. S. 1910, p. 26 (April 26).

Darker than *M. inez*, with a longer and more distinctly bicolor tail.

General colour above decidedly darker than in *inez*, the back approaching "Prout's brown"; under surface also brown, of a slightly more buffy tone than the upper surface, but not sharply

\* The complete account of the new species described in this communication appears here, but since the names and preliminary diagnoses were published in the 'Abstract,' No. 83, 1910, these species are distinguished by the names being underlined.—EDITOR.

† P. Biol. Soc. Wash. xiii, p. 155, 1900.

separated from it, the belly on the average decidedly browner than in *inez*. Head rather greyer. Hands and feet dull whitish or pale brown, averaging rather darker than in *inez*. Tail longer than in that species (average of 17 specimens 38 mm. as against 33 mm. in 14 *inez*), bicolor, dark brown or blackish above, dull whitish below.

Skull agreeing closely with that of *M. inez*, except that the posterior lateral palatal grooves tend to be deeper and more continuous, and thus to show an approach towards the single deep depression found on each side in *melanogaster*. Bullæ large, larger than in either of the other species.

Teeth on the whole most like those of *M. inez*, but showing an approach towards those of *melanogaster* by the junction of several of the enamel spaces, closed in the former, open in the latter. Thus in  $m^3$  the normal 2nd and 3rd spaces, separated in *inez*, are joined as in *melanogaster*, and in  $m_1$  the two spaces next following the trefoil are frequently joined to each other as in *Pitymys*. Small extra internal projection on  $m^1$  and  $m^2$  as in *M. inez*.

Dimensions of the type, measured in the flesh :—

Head and body 93 mm.; tail 39; hind foot 16.5; ear 10.

Skull: condylo-basal length 23.6 mm.; greatest breadth 14.3; nasals 7; interorbital breadth 4; palatilar length 11; diastema 6.5; palatal foramina 4.7; bullæ, diagonal horizontal diameter 7; upper molar series 5.6.

*Hab.* of type. Shang-chou; S.E. Shen-si. 3300'.

*Type.* Adult male. B. M. No. 10.5.2.79. Original number 2089. Collected 29 November, 1909. 23 specimens.

The discovery of this interesting species tends to confirm the reference of *M. inez* to *Eothenomys*, about which I had some doubt. For while *M. melanogaster*, the type of *Eothenomys*, has nearly all its cement-spaces communicating with each other, and *M. inez* has them nearly all closed and separate, the present form differs from *M. inez* exactly in the direction of *melanogaster* by the opening of several of the spaces, the great majority of them being still closed.

#### MICROTUS JOHANNES Thos.

Abstract P. Z. S. 1910, p. 26 (April 26).

Near *M. mandarinus*, but rather smaller, with much smaller skull.

General characters very much as in *M. mandarinus*. Fur soft and fine; hairs of back about 11–13 mm. in length. General colour above rather browner than Ridgway's wood-brown, decidedly paler than in *M. mandarinus*. Under surface dull greyish; the hairs slaty basally, greyish white terminally. Ears short, projecting but slightly above the fur; practically naked. Upper surface of hands and feet dull whitish. Tail short, drabby whitish above, dull white below.

Skull broad and flat, very like that of *M. mandarinus* on a smaller scale. Brain-case square, with well-marked angles, but the ridges little developed. Anterior palatine foramina of about equal breadth throughout, those of *mandarinus* broad in front, narrowing behind.

Incisors markedly lighter than in *mandarinus*, their faces orange to the tips. Molar pattern about as in *M. mandarinus*;  $m^3$  with 4 spaces, three outer and three inner salient angles;  $m_1$  with 7 spaces, 5 inner and 4 outer angles. All triangles separated from each other except in  $m_3$ .

Dimensions of the type, measured in the flesh:—

Head and body 95 mm.; tail 23; hind foot 17; ear 7.

Skull: condylo-basal length 24.6 mm.; greatest breadth 15.2; nasals  $7.0 \times 3.1$ ; interorbital breadth 3.5; palatilar length 13.2; diastema 7.1; palatal foramina 4.1; upper molar series (crowns) 5.8.

*Hab.* Mts. 12 miles N.W. of Ko-lan-chow, Shan-si. Alt. 7000'.

*Type.* Adult male. B.M. No. 9.1.1.178. Original number 1950. Collected 5 June, 1908.

This Vole was referred to *M. mandarinus* M.-Edw. in my last paper \*, but by the kindness of Prof. Trouessart I have had an opportunity of re-examining the skull of that species, and I find it to agree in every detail with two specimens now sent from Shang-chow, S.E. Shen-si, and to differ equally from the Ko-lan-chow form, which therefore needs describing.

If, however, this identification be accepted, it throws some doubt on the asserted locality of "Mongolie chinoise" for *mandarinus*, and I think it not impossible that the type really came from S. Shen-si, where David made a small collection, after getting his Mongolian series.

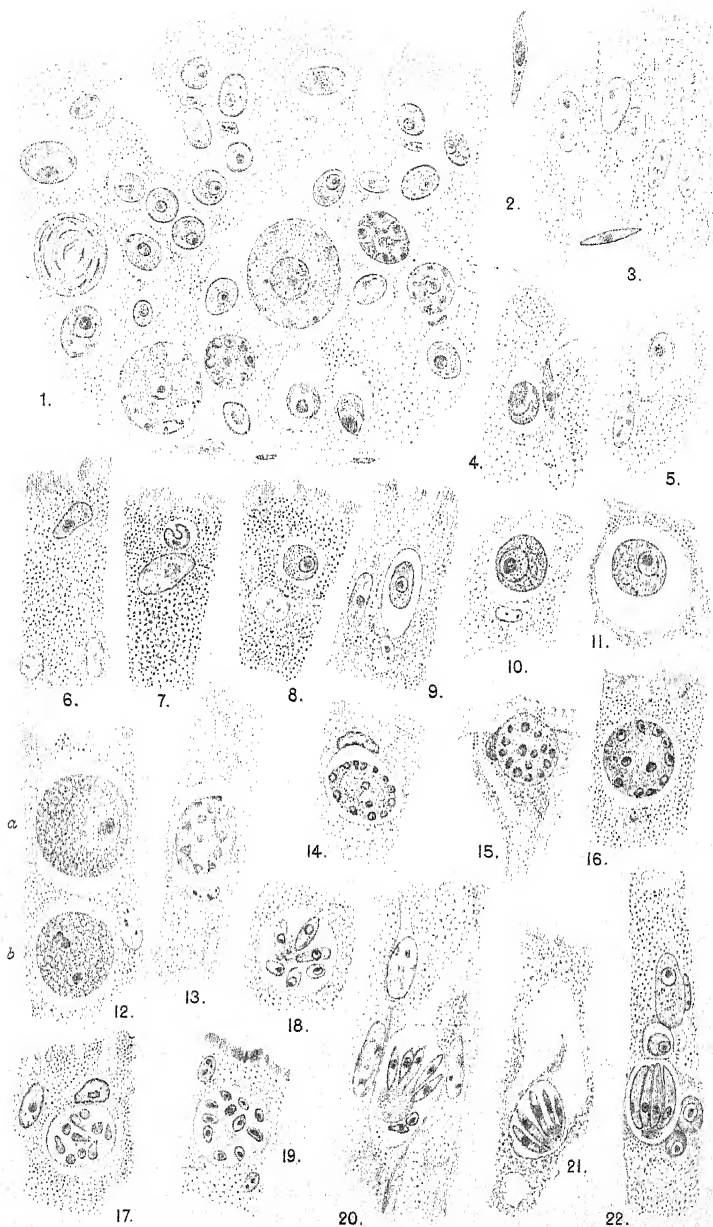
*M. johannes* is readily distinguishable from *M. mandarinus* by its paler colour and markedly smaller skull.

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Mr. J. Lewis Bonhote, M.A., F.L.S., F.Z.S., exhibited a yellow variety of *Mus rattus*. This individual had been bred from two wild-caught examples of *Mus rattus tectorum* from Egypt. The long hairs on the upper parts, which are normally black, were colourless and the shorter body-hairs had grey bases with yellow tips. So far as he knew, this was the first recorded example of a yellow rat, which was a colour quite unknown to fanciers and was never met with by Crampe or Doncaster, who had conducted colour-breeding experiments on rats. Although it was not definitely stated, these experiments had probably been carried out with *Mus norvegicus*. A careful search through the large series of *Mus rattus* in the Museum also failed to bring to light any yellow forms.

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\* P. Z. S. 1908, p. 976.



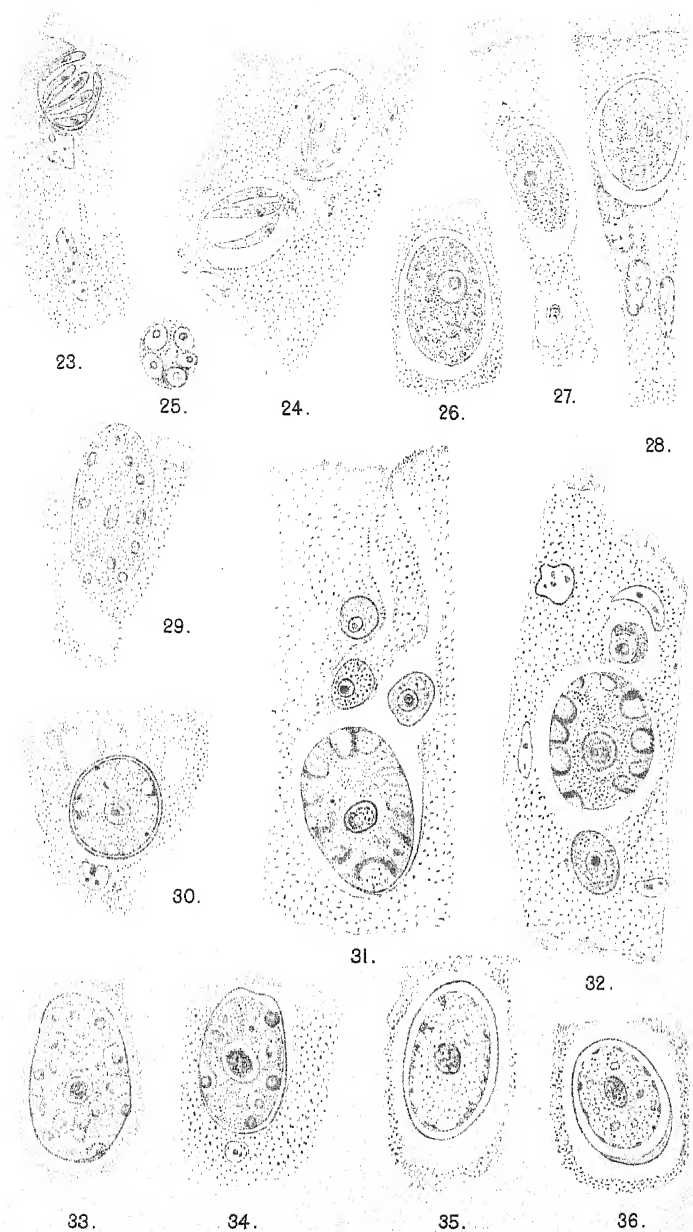
H.B. Fantham del.

E. Wilson, Cambridge.

*EIMERIA (COCCIDIUM) AVIUM.*  
(Schizogony)





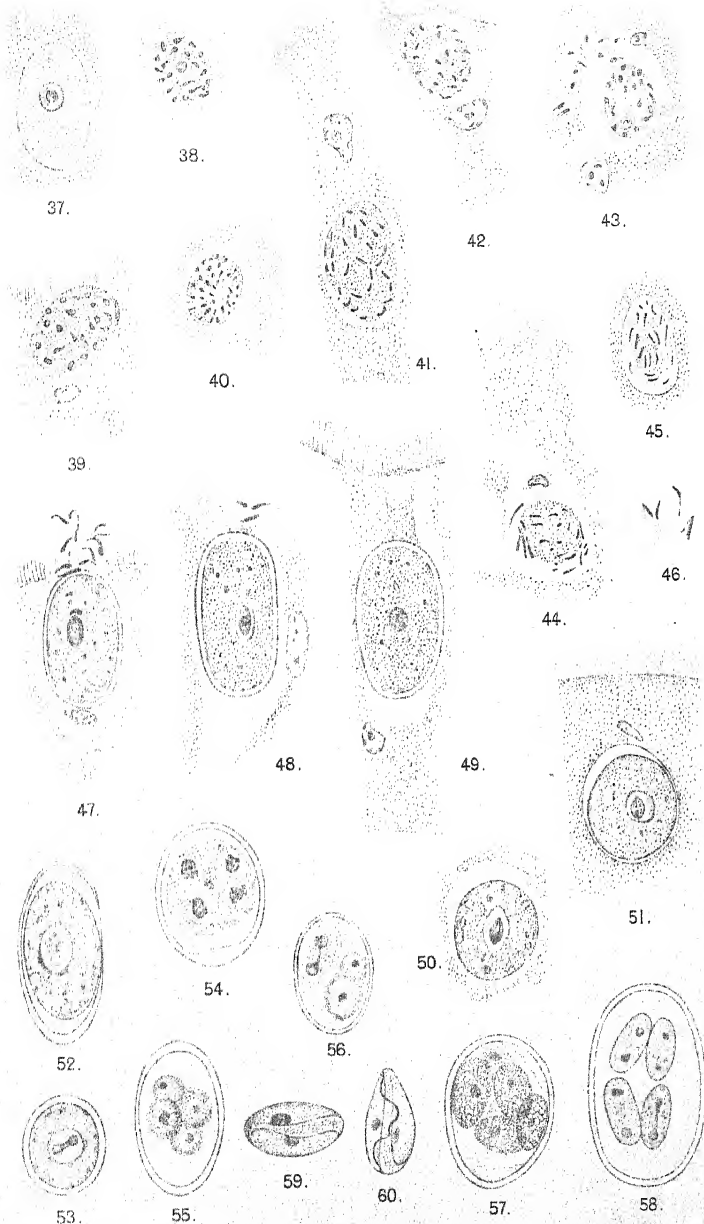


H.B.Fantham del.

E. Wilson, Cambridge

*EIMERIA (COCCIDIUM) AVIUM.*  
(Macrogamete formation.)

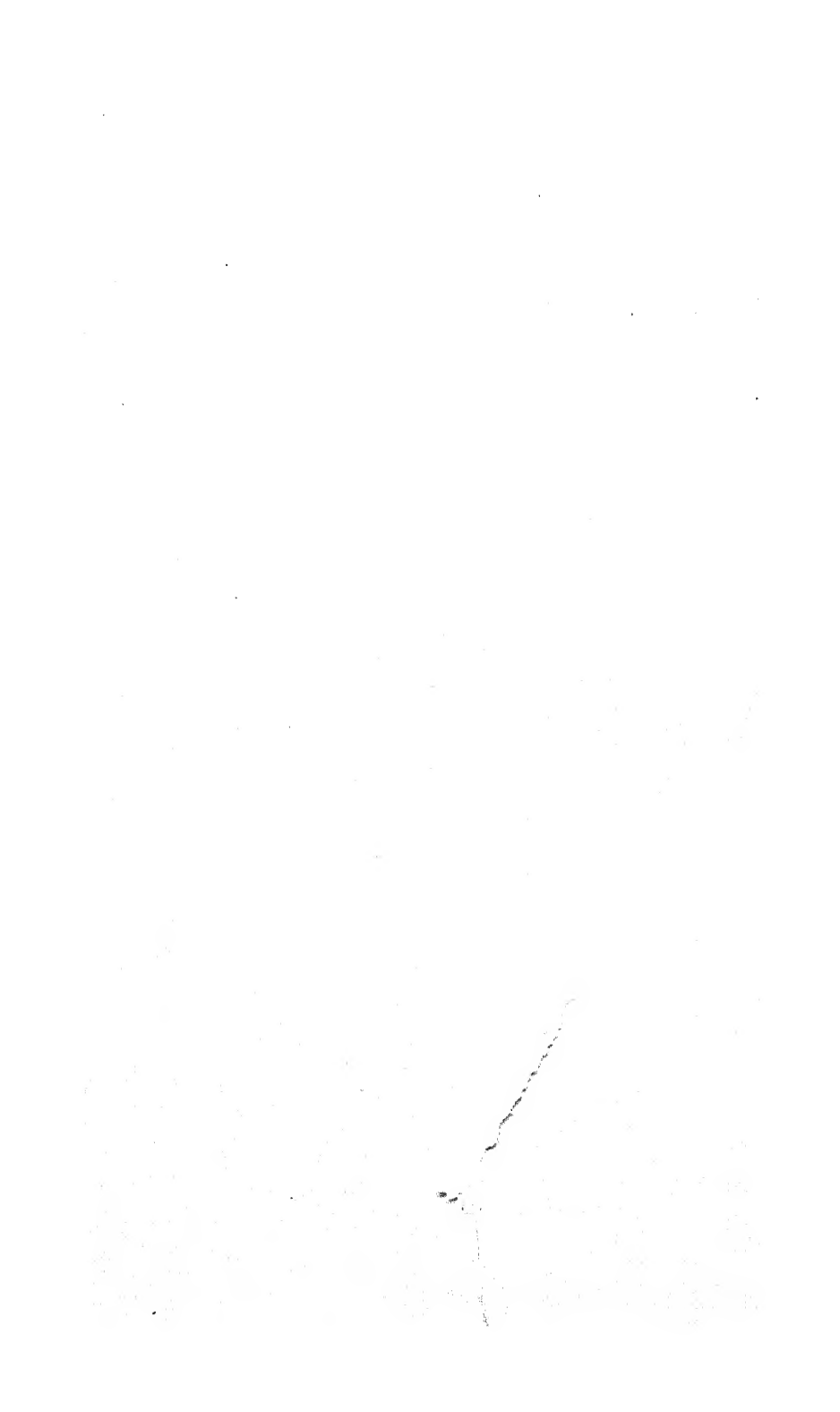


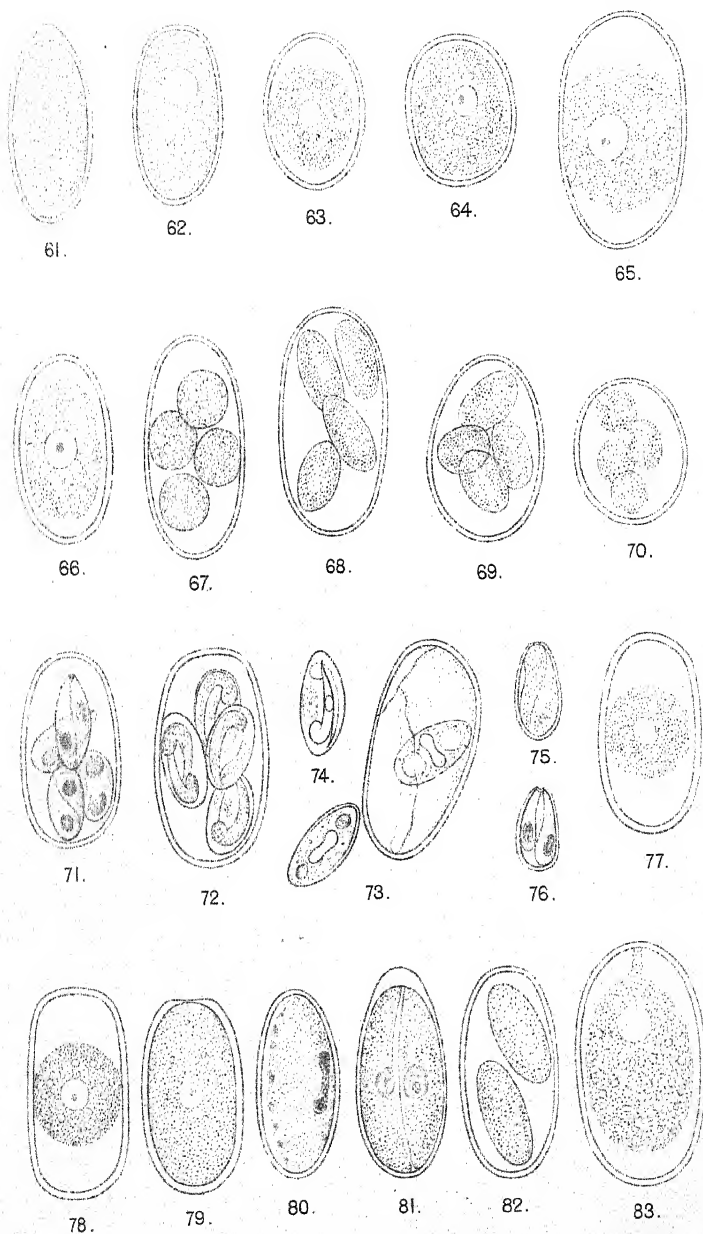


H. B. Fitch del.

E. Wilson, Cambridge

**EIMERIA (COCCIDIUM) AVIUM.**  
(Microgametes, Sporogony.)





H.B. Fantham del.

*EIMERIA (COCCIDIUM) AVIUM.*  
(Sporogony.)

E. Wilson, Cambridge.



resistant spores adapted for life outside the body of the host. The spores so formed are the means of spreading the parasite and lead to the infection of fresh hosts. The two phases were formerly considered to belong to separate parasites; but the occurrence of alternation of generations in the life-cycle of Coccidia was first suggested by R. Pfeiffer in 1892, conjugation was discovered in Coccidia by Schaudinn and Siedlecki (1897), and the complete life-cycle was demonstrated with a wealth of morphological and cytological detail in the celebrated memoir of the late Dr. Schaudinn (1900) on *Eimeria* (*Coccidium*) *schubergi*, parasitic in the gut of the centipede *Lithobius forficatus*.

Coccidia have been recorded from most of the great groups of the Metazoa, but very few Coccidian life-histories have been investigated completely.

Dr. Leiper, while working on helminthiasis in grouse in May 1909, noticed the occurrence of Coccidian cysts in large numbers in the gut of many grouse-chicks, with concomitant enteritis, very often proving fatal. The Coccidian cysts are oval and, at first sight, might easily be mistaken for eggs of worms. Leiper suggested that coccidiosis was a factor in "grouse disease," especially in young birds. Through the courtesy of Lord Lovat I was enabled to spend a few days early in June 1909 on a Scotch moor to investigate coccidiosis in grouse chicks\*. Previously we had noticed, at various times, the occurrence of Coccidian cysts in adult grouse, but not in large numbers.

I have much pleasure in expressing my thanks to Lord Lovat, Dr. A. E. Shipley, Dr. E. A. Wilson, Dr. Hammond Smith, and Dr. Leiper for aiding my researches by procuring material for me, and to Professor Nuttall, in whose laboratory much of my work was done. I would also thank Mr. A. S. Leslie for placing me in communication with correspondents, and to members of the Grouse Disease Inquiry and many correspondents I am also indebted.

In this paper I wish to record my researches on the morphology and life-history of *Eimeria avium*, more especially as it occurs in the grouse. I would point out that the length of time at my disposal for these researches has been limited, only *one* season being available to me for procuring material, and I have had several other investigations to consider during the period, so that I was not able to give undivided attention to the elucidation of the Protozoa of grouse. However, the complete life-cycle of *Eimeria avium*, responsible for the dwindling of grouse broods in spring, is here set forth for the first time, so far as I am aware.

## II. THE GENERIC NAMES *EIMERIA* AND *COCCIDIUM*.

Unfortunately, owing to the rule of priority, the generic name *Coccidium* (Leuckart 1879) no longer holds, but is replaced by that of *Eimeria* (A. Schneider 1875). I am in sympathy with

\* The number of grouse chicks dying of coccidiosis on the moors is not easily estimated, for the chicks die in the heather, and their tiny corpses are rarely found.



Professor Minchin when he writes in a recent review:—"We regret to see the familiar generic name *Coccidium* replaced by *Eimeria*; this is one of those many cases where, in our opinion, rebellion against the law of priority in nomenclature is not only lawful but imperative" ('Nature,' March 3, 1910). It would save much confusion if the question of zoological nomenclature were settled by an international committee, as has been suggested by many able workers.

The *Coccidia* of birds were first recorded in fowls by Silvestrini and Rivolta (1873), under the name *Psorospermium arium*. Subsequently Railliet and Lucet (1891) recorded *Coccidia* from fowls, naming the parasite *C. tenellum*. I have followed Doflein (1909) in naming the *Coccidia* of birds *Eimeria arium*. The *Coccidian* parasites were obtained from grouse chicks, and I have succeeded in transmitting the *Coccidia* of grouse to fowl chicks and to young pigeons.

### III. METHODS.

In this investigation of coccidiosis both fresh and preserved materials were used. Samples of gut contents, taken from different regions, were examined fresh, and often these have been fixed wet with osmic or formalin vapour and stained by Delafield's hamatoxylin or by Giemsa's stain. Such smears were sometimes useful for examining merozoites.

Oöcysts, because of the chitinous and almost impenetrable character of their walls, had to be examined fresh.

For preserved material, the best fixatives were found to be Schaudinn's fluid (corrosive-acetic-alcohol), and Bouin's fluid (picro-formol-acetic) to which a few drops of absolute alcohol were added. Schaudinn's fluid tends to shrink the tissues, while Bouin's fluid requires much washing out. Sections,  $5\mu$  to  $6\mu$  thick, were made of the duodenum and caecum of infected birds, these parts of the digestive tract being especially examined. The chief stains used were Delafield's hamatoxylin (either alone or counterstained with Orange G or eosin), which was found to be most useful, safranin and Lichtgrün, iron-hamatoxylin (with or without van Gieson's picro-fuchsin) and pararcarmine. On the whole the hamatoxylin proved of most service.

### IV. MORPHOLOGY.

On diluting some of the caecal contents or faeces of a grouse chick suffering from coccidiosis, and examining the preparation microscopically, numerous oval cysts are seen (Pl. LVIII, figs. 61-66). Sometimes the cysts are also seen in the small intestine just beyond the duodenum. These cysts may have homogeneous contents, or, when older, may show four more or less well differentiated sporozoites within them (figs. 67-70). Each sporozoite, if ingested by another grouse, can develop two active, motile germs or sporozoites (figs. 71-76), which can penetrate

the intestinal epithelium—especially of the duodenum—and so begin a new infection. Though the oöcysts and spores are the most obvious external manifestation of coccidiosis, it is usual and certainly more convenient to begin the life-cycle of the *Coccidium* with the minute sporozoite (Pl. LV. fig. 2), the agent whereby primary infection is brought about.

(a) *The young, growing Parasite.*

The sporozoites are minute, falciform or vermicular bodies (Pl. LV. fig. 2) capable of fairly rapid movement and possessing great penetrative powers. They measure from  $7\mu$  to  $10\mu$  in length. The ends of the sporozoite are rather pointed, the extremity that moves foremost being slightly more acuminate than the posterior end. The general body cytoplasm is more or less homogeneous, exhibiting but very fine granulations. The nucleus has a definite rounded or oval contour. The chromatin is evenly distributed throughout the nucleus.

When the sporozoites are liberated from the investing sporocyst (Pl. LVIII. figs. 74–76), by the action of the pancreatic juice of the grouse, they are capable of active movement. The usual method of progression resembles that of the sporozoite or motile trophozoite of a Gregarine. The organism moves forwards with a slow gliding movement, the forward progression being facilitated by the secretion of a viscid proteid substance that rapidly hardens. On the smooth surface thus provided the coccidian sporozoite glides forward. The track of the sporozoite, as shown by its trail, can be stained, and the organism then shows the gelatinous or proteid material issuing from near the posterior region of its body (Pl. LV. fig. 2). During the gliding movement waves travel down the body of the sporozoite, recalling what is seen on a larger scale in the billowy undulations of the foot of a snail. On other occasions a more rapid movement of the sporozoite occurs. The two ends of the organism become approximated and then rapidly straightened, the effect being to propel the organism forwards much more quickly than when the gliding movement alone is used.

The sporozoite thus makes its way to an epithelial cell of the duodenum and proceeds to penetrate the cell. As it forces its way inwards (Pl. LV. figs. 3, 4), so the sporozoite curves on itself (fig. 7) and becomes round and immobile (figs. 5, 6, 8). The young, rounded parasite (figs. 8–10) is now in the trophic phase of existence and continues to grow for some time, feeding passively on the food-materials of the host-cell. During this period the parasite is called a trophozoite (figs. 8–12 a).

The nucleus of the trophozoite is approximately central in position, or sometimes to one side, and at first contains scattered granules of chromatin. It then becomes somewhat vesicular (figs. 8–11), and gradually the chromatin collects into a central karyosome, lying within the nuclear sap (fig. 12 a). The position

of the karyosome, however, is not centrally fixed; it may lie to one side of the nucleus (figs. 8, 10).

The growth of the trophozoite naturally affects that of the host-cell. The protoplasm of the latter becomes more and more tenuous, great hypertrophy of the host-cell occurring. This condition is maintained for some time and finally a limit is reached and atrophy sets in, the nucleus of the host-cell then appearing as a small, often crescentic mass (figs. 10, 14) to one side of the film (fig. 12) that represents the host-cell. A clear space often intervenes between the parasite and the enveloping epithelial film (figs. 9, 11, 12).

The trophozoite, having attained its full size (some  $10\mu$  to  $12\mu$  in diameter) within the host-cell, proceeds to divide, and the result of its division is to increase the number of parasites within the host. This stage in the existence of *Eimeria arium* is known as the schizont (agumont), and the method of multiplication is termed schizogony.

#### (b) *Schizogony.*

The schizont (fig. 12) is a more or less spherical parasite. At first it is uninucleate (fig. 12 a), but soon its nucleus begins to fragment (fig. 12 b). The division of the nucleus of the schizont is of the nature of multiple fragmentation rather than of a series of binary fissions of the nucleus and karyosome (figs. 13-18). The parasite is very small and it is not easy to follow the cytological details, even under the best and highest powers of magnification. Some of the portions of chromatin in multiple fragmentation may sometimes appear connected by thin strands (fig. 13) for a short period, but the fragments soon travel to the periphery of the schizont. The small daughter masses of chromatin, at first homogeneous, gradually show differentiation, becoming minutely vesicular with a dot of chromatin usually to one side (figs. 14-16), but occasionally central. Thus the nuclei of the future merozoites are forming their karyosomes early.

The daughter nuclei having migrated to the periphery of the mother cell (fig. 16), the cytoplasm of the schizont concentrates around them forming small ovoid masses (figs. 18, 19). The daughter forms so produced are the merozoites (agametes) which measure  $6\mu$  to  $10\mu$  in length. They gradually acquire a vermiform shape and arrange themselves around the remains of the protoplasm of the mother cell like the segments of an orange or the staves of a barrel (Pl. LV, figs. 20-22, Pl. LVI, figs. 23, 24). Owing to this method of grouping, the merozoites are said to be arranged "en barillet." The groups, when ripe, soon break up and the individual merozoites are liberated. The movements of the merozoites, when free, resemble those of the sporozoites.

The number of merozoites formed from a single schizont seems to vary. Eight to fourteen seem to be common numbers, but as many as twenty have been found.

The merozoites finally are slightly curved vermicules (Pl. LVI, figs. 23, 24), possessing a nucleus which may be approximately

central (Pl. LV. figs. 20, 21) or somewhat towards one end (Pl. LV. fig. 22, Pl. LVI. fig. 23). The nucleus of the merozoite is small, and the presence of a karyosome is often not very evident, though there is a small granule of chromatin—representing the karyosome—usually to one side of the nucleus (fig. 24). The ends of the merozoites are rather less pointed than those of the sporozoites, a feature that *E. acium* has in common with *E. schubergi* as described by Schaudinn.

When the merozoites reach a new host-cell, they enter, become round, and proceed to grow as trophozoites in the same way as did their parent organism, and undergo later nuclear fragmentation in a similar manner. As the result of this, many more merozoites are produced, and as schizogony may be continued through several generations, the destruction of the gut epithelium is very extensive (Pl. LV. fig. 1).

Towards the end of schizogony—especially in the cæcum—relatively smaller schizonts with larger and fewer merozoites (fig. 25), about five in number on the average, are produced. These larger merozoites appear to be formed near the end of infection, in company with large numbers of gametocytes, so far as evidence is available.

These differences in the schizonts might be taken by some investigators to be indicative of difference of species—in other words, that more than one species of *Coccidium* may occur in the gut of grouse. I do not state that this is not so, but personally prefer the view that the differences in the schizonts and merozoites noted are reflexes of the condition of nutriment of the parasite. Wenyon (1907) has some interesting observations on the variations in the schizogony of *E. falciformis* in the mouse, and states that the variations are due to the nourishment available for the parasite. Again, the species found in the liver and gut of the rabbit (*Coccidium oriforme* and *C. perforans*) are now usually united into one species, *Eimeria stiedæ*.

The merozoites originally produced in the duodenum pass lower down the gut and reach the cæca. At the ileo-cæcal junction, the epithelium is attacked again, and the merozoites rapidly grow to schizonts which produce new generations of merozoites, so that the cæca soon contain very large numbers of the parasites.

Probably coccidiosis set up in the duodenal wall is sufficient to kill very young chicks, *e.g.* chicks 8 to 10 days old, while older chicks dying at the age of about 4 to 6 weeks may have partially recovered from duodenal coccidiosis, but succumb to coccidiosis in the cæcum (typhlitic coccidiosis). In cases of intense duodenal coccidiosis, merozoites are found free in the intestinal contents and even in freshly shed fæces.

Sooner or later a limit is reached, both to the power of the grouse chick to provide nourishment for the parasite, and to the multiplicative capacity of the parasite itself. In other words, the host begins to react on the parasite. Consequent on the now unfavourable environment, the parasite proceeds to form gametes, in order that its species may be perpetuated. The

gametocytes or mother cells of the gametes (Pl. LVI. figs. 26-28, Pl. LVII. fig. 37) are modified schizonts which are of slow growth, and therefore can accumulate more reserve food-material in the form of granules within their cytoplasm. The processes leading to the formation of the gametes may be termed gametogony, which we may now consider.

### (c) *Gametogony.*

Sexual differentiation is characteristic of the gametes of Coccidia, and in the case of *Eimeria avium* the differentiation is apparent in the gametocyte phase. Two forms of gametocytes can be distinguished. The first group are intra-cellular parasites containing large granules of food reserve within their cytoplasm. These are the macrogametocytes (Pl. LVI. fig. 26) which give rise each to one female gamete. On the other hand, the microgametocytes (Pl. LVII. fig. 37) or male progenitors contain a little reserve food-material in the form of very minute granules, distributed evenly throughout the body substance. Each microgametocyte gives rise to many microgametes.

#### *The Macrogametocyte and Macrogamete.*

The structure of the macrogametocyte and of the single macrogamete that arises from it is very difficult of interpretation in *Eimeria avium*, on account of the large amount of reserve food-material contained within the cytoplasm. Further, it is very difficult to draw the exact dividing line between the macrogametocyte and the female gamete, as the one gradually merges into the other. These forms vary from  $11.8\mu$ – $17.5\mu$  in length, by  $6\mu$ – $11\mu$  in breadth, as seen in sections. Many relatively large granules occur in the cytoplasm of the macrogametocyte. As the macrogametocyte grows from round to ovoid, these granules gradually concentrate to form larger, roundish, hæmatoxylin-staining granules, which are albuminoid (Pl. LVI. fig. 29), the chromatoid granules of many authors. There are also other, non-basic staining, granules known as plastinoid granules ("granules plastiques" of Thélohan and Labbé) composed of coccidin (Labbé). These ultimately are large and round (figs. 30–32) and are refractile in fresh preparations, where they appear yellow or greyish-green. They tend to shrink in preparations fixed with sublimate or sublimate acetic (fig. 29). The plastinoid granules occur between and among the chromatoid granules (figs. 30–32). In stained preparations\* the granules are best seen by staining with iron-hæmatoxylin followed by van Gieson's picro-fuchsin, when the chromatoid granules appear blackish, while the plastinoid granules take on a uniform, yellowish hue. The plastinoid

\* The reactions of the granules are discussed by Labbé (1896) and by Minchin (1903).

granules stain with Lichtgrün in marked contrast with the red of safranin taken up by the chromatoid granules. With Delafield's hæmatoxylin, the chromatoid granules stain intensely (figs. 29, 31, 32), and somewhat misleading appearances result, suggesting multiplication of the cell.

As the parasite grows, the chromatoid and plastinoid granules travel towards the periphery (figs. 29-32). The macrogametocyte at this time encysts within the epithelium, and the chitinous material of the cyst seems to be formed from the chromatoid granules. At any rate, the inner layer of the cyst-wall seems to take its origin therefrom (figs. 34-36). The formation of the cyst-wall from the chromatoid granules has been noted by Simond (1897) and Wasielewski (1904) in the case of *Coccidium oviforme* (*Eimeria stiedæ* of Stiles).

The formation of the cyst of *Eimeria avium* takes place while the organism is still within the epithelium (figs. 34, 35), and therefore the parasite encysts precociously. The macrogamete at this stage is ovoid, and the number of chromatoid granules within it is reduced. The cyst formed is ultimately rather thick-walled, but a small aperture or micropyle, which may be in a slight depression, is left for the entry of the microgamete (Pl. LVII. fig. 47).

When Schaudinn investigated the life cycle of *E. schubergi*, he described a process of maturation of the macrogametocyte, whereby the karyosome of the nucleus was expelled in fragments. I regret that I am not at all sure as to the fate of the karyosome of the macrogametocyte of *E. avium*. Several causes combine to defeat the attempts made to elucidate this subject. In the first place, the entire parasite (*E. avium*) is much smaller than *E. schubergi* and its karyosome is not nearly so well differentiated a structure. Further, the presence of the chromatoid granules, which stain deeply with basic stains, much confuses the structure. Similar causes prevail in *E. oviforme* (*E. stiedæ*), as I can vouch from personal observation, and Wasielewski (1904, p. 54) states that he is unable to follow the maturation process in *E. oviforme*.

It may be that *E. avium* is like some other *Coccidia* (e. g. *C. lacazei*, *C. proprium*, *Adelea ovata*) where the karyosome is retained in the gamete and is left behind in the residual protoplasm of the oöcyst. On a few occasions, I have observed a small, chromatin-like granule in the oöcyst residuum (Pl. LVII. fig. 57), and this body may be the karyosome of the macrogametocyte. *E. avium* is distinguished by having a very small cystal residuum, which, together with the smallness of the karyosome, and indeed of the whole parasite, increases the difficulty of investigation. However, at the time of fertilisation, the distinctness of the karyosome of the macrogamete has disappeared (Pl. LVI. figs. 29-36), and the nucleus of the macrogamete appears to contain granules of chromatin which are rather indistinct.

*The Microgametocyte and Microgametes.*

The microgametocyte\* (Pl. LVII. fig. 37) is an ovoid cell about  $13\ \mu$  long and  $8\ \mu$  broad in the specimens that I have seen. It possesses a central nucleus containing a karyosome. The process of the formation of the microgametes of *E. avium* is as follows:—The chromatin of the nucleus, largely concentrated in the karyosome, breaks up (figs. 38–40) into minute granules or chromidia which pass towards the surface of the cell, where they appear to form a *very* fine chromidial network (fig. 38). The chromidia then collect into groups or patches, arranged in the form of minute, irregular loops with central hollows (figs. 38, 39). These chromatic loops form a number of minute, flexible, rod-like bodies, composed almost entirely of chromatin (figs. 41–45). These are the young microgametes (figs. 43–46). The adult microgametes are small parasites, their chromatic bodies measuring  $3\ \mu$  to  $4\ \mu$  in length, possessing a rod-like, somewhat curved body composed of a core of chromatin which is surrounded by a tenuous film of cytoplasm, prolonged outwards to form two fine flagella (figs. 44, 46). The flagellum which I term the posterior flagellum trails behind the organism and is practically a continuation of its body; the other flagellum is at the opposite end of the body and so is termed the anterior flagellum. In life, the microgametes are capable of serpentiform movements. Owing to the minute size of the microgamete (about  $3\ \mu$  to  $4\ \mu$  long) it is only with the greatest difficulty that the flagella can be discerned.

The whole of the microgametocyte is not used in the formation of the microgametes. When separation of the microgametes from their mother cell occurs, a large amount of the body-substance of the latter remains as a somewhat faint staining residuum, in which the pale staining remains of the karyosome (fig. 43, cf. fig. 38) can sometimes be distinguished. The residuum takes no further part in the vital activities of the parasite.

The microgametes are set free into the lumen of the gut and proceed to seek out the macrogametes.

*(d) Fertilisation.*

When the macrogamete has attained its maximum development, it often lies in the epithelium, near the outer edge of the tissue, or may even burst through the attenuate wall of the host-cell and so reach the margin of the lumen of the gut. The minute but active microgametes (Pl. LVII. fig. 46) meanwhile have broken away from the residual protoplasm of the host-cell, and swum out with rapid lashing movements of their flagella into the gut. Here they are attracted, possibly by some chemiotactic substance,

\* Uninucleate microgametocytes seemed rare in preparations, for the cell rapidly proceeds to form many microgametes.







Huth, coll.

PHOTOPHORES OF ACANTHEPHYRA DEBILIS.

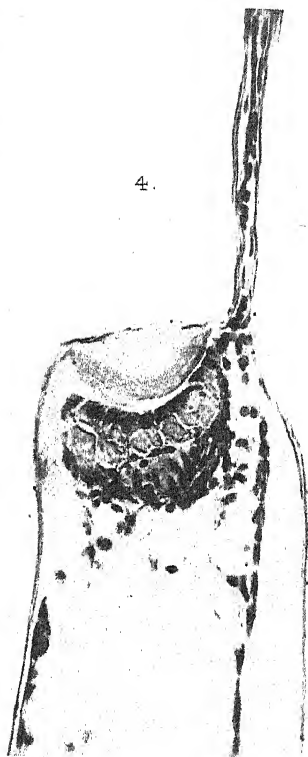




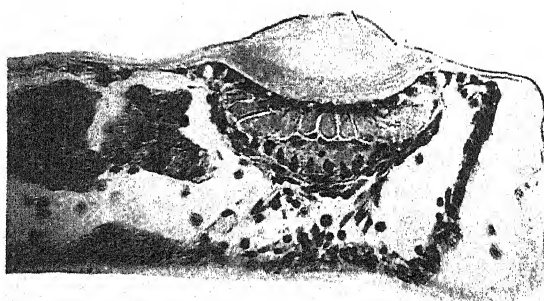
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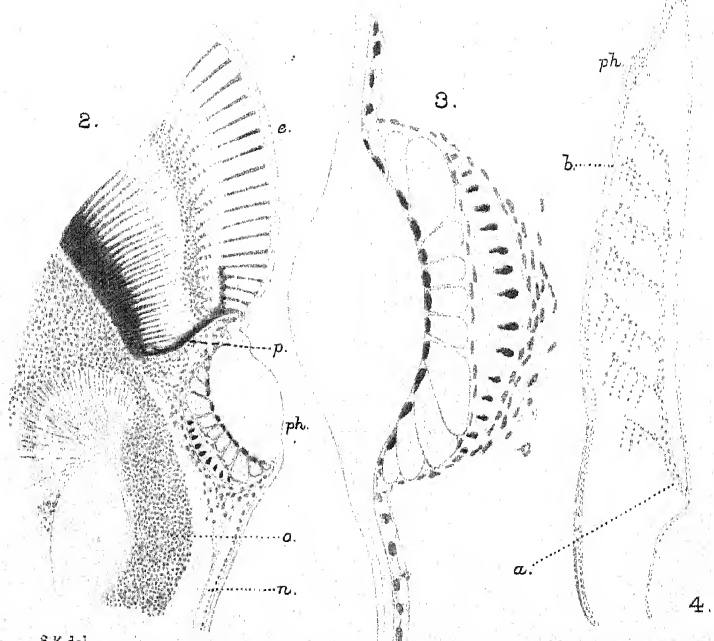
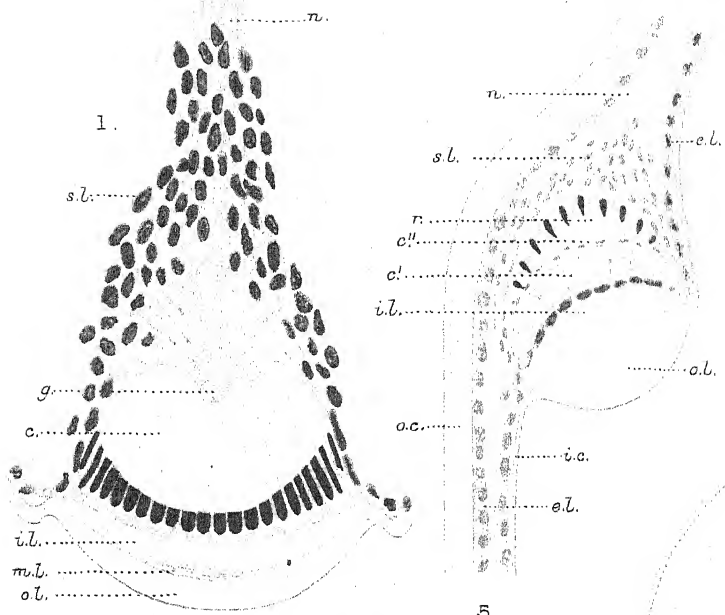


3.

PHOTOPHORES OF ACANTHEPHYRA (Fig. 1)  
AND SERGESTES (Figs. 2-4).

Rath, coll.





S.K. del.

Hutch. Litho London.

PHOTOPHORES OF ACANTHEPHYRA (Fig. 1)  
AND SERGESTES (Figs. 2 - 5).

*Centenary of Philip Henry Gosse, F.R.S.  
Born April 6, 1810; died Aug. 23, 1888.*

The Secretary exhibited the set of the works of Philip Henry Gosse in the Society's Library and gave a brief summary of his contributions to science, upon which he placed a very high value. The Chairman and Prof. A. Sedgwick, F.R.S., added their testimony to his place in Zoological history; Dr. Henry Woodward, F.R.S., gave some personal reminiscences; and Mr. Edmund Gosse, Librarian of the House of Lords, the son and biographer of Gosse, thanked the Society for their notice of his father's centenary.

The following papers were read:—

1. Notes on the Photophores of Decapod Crustacea.

By STANLEY KEMP, B.A.\*

[Received March 1, 1910.]

(Plates LII.—LIV.†)

Two different methods of producing light are known among Crustacea. In the vast majority of species possessing this power the organ is of a glandular nature, excreting drops of oily fluid which become luminous on reaching the water. The process is probably one of oxidation, though from the results of Giesbrecht's experiments‡ it would seem that very small quantities of free oxygen will suffice.

Certain Decapods, such as *Polycheles phosphorus*, appear to produce light in this way, while in others, such as *Aristeus coruscans* and *Heterocarpus alphonssi*, the excretions from the antennal glands have been noticed to be brilliantly phosphorescent §. Both these phenomena seem to be exceedingly rare among Decapods.

The second method of producing light, and it is only with this type that the present paper is concerned, is by means of photophores, compound luminous organs which do not excrete a fluid; they are in most cases provided with a lens and sometimes also with a reflector. Very little is known of the chemical processes which are involved in this type of phosphorescence. The essential feature, as in the case of the glandular organs, is doubtless one of oxidation, and it is probable, as Alcock has suggested, that the oxygen is conveyed to the photophore by means of the blood.

Among Crustacea, photophores are known only in the Euphausiacea and in the Decapoda. In the former group they are very highly specialised and occur in practically all the species known.

\* Communicated by Dr. W. T. CALMAN, F.Z.S.

† For explanation of the Plates see p. 650.

‡ Giesbrecht, Mitth. Zool.-Stat. Neapel, ii. 1895, p. 648.

§ See Alcock, 'A Naturalist in Indian Seas,' 1902, pp. 134 & 135.

Their true function was first demonstrated by Sars \*, and their structure is now well known owing to the work of Chun † and of Vallentin and Cunningham ‡.

Photophores occur only in three genera of Decapoda, all of which belong to the Macrura, or, according to modern systems of classification, to the Natantia. One of them, *Sergestes*, belongs to the Penæidea, and the other two, *Acantheephyra* and *Hoplophorus*, to the Caridea. Although, as might be expected, two wholly different types of structure are found in these two groups, they have none the less one very striking feature in common—in both a deep blue pigment is associated with the luminous organ. This pigmentation is one of the most interesting characteristics of the photophores of Decapoda, for, except for the fact that it has once been observed in a Euphausian, such an association appears to be elsewhere unknown.

The following six species of Decapods possess photophores :—

#### PENÆIDEA.

Sergestidæ..... *Sergestes challenger*i Hansen.  
*Sergestes gloriosus* Stebbing.

#### CARIDEA.

Hoplophoridæ ... *Acantheephyra pellucida* Perrier.  
*Acantheephyra debilis* A. Milne-Edwards,  
*Hoplophorus grimaldii* Coutière.  
*Hoplophorus* sp. juv.

Two other genera, *Gennadas* and *Amalopenceus*, belonging to the family Penæidæ, may also possess photophores, but it has not as yet been possible to come to any definite conclusion on the subject.

The material which I have been able to examine consists of one species of each of the three genera mentioned above. I am indebted to Prof. J. Stanley Gardiner for the opportunity of examining four specimens of *Sergestes challenger*i and an immature *Hoplophorus* from the Indian Ocean. The examples of the former genus are preserved in formalin and have in consequence retained some at least of their original pigmentation. *Acantheephyra debilis* occurs in all stages off the West coast of Ireland. This species is unfortunately far from common, and although special efforts have been made, no fresh material has been found during the last eighteen months. In consequence, it has not been possible to solve certain problems connected with the pigmentation and innervation of the photophores.

Deep-sea Decapods are almost invariably dead when brought to the surface, and although in view of recent investigations it does not seem probable that the vitality of the organism has

\* Sars, Report on the 'Challenger' Schizopoda, 1885, p. 70.

† Chun, Bibliotheca Zoologica, Bd. vii. (Heft 19), 1896, p. 191.

‡ Valtentin & Cunningham, Q. J. Micr. Sci. xxviii. 1888, p. 319.

any direct effect on the production of light, it is none the less the case that phosphorescence has actually been observed only in a single species, *Sergestes challengerii*. Prof. Gardiner informs me that the examples of this form which he obtained in the Indian Ocean were brilliantly phosphorescent on the occasion of their capture. In the other species the function of the organs has been deduced from their structure only.

#### THE PHOTOPHORES OF *SERGESTES*.

The only two species of *Sergestes* which are known to possess photophores are *S. challengerii*, which was described by Hansen\* from a single specimen obtained by the 'Challenger' Expedition near the Fiji Islands, and a closely allied form, *S. gloriosus* Stebbing†, which was found in South African waters. Hansen discovered 117 photophores in his mutilated example of *S. challengerii*, and estimated that at least 150 would be found in a perfect specimen. According to Stebbing's account an even greater number exist in *S. gloriosus*.

It is not necessary to describe the distribution of the photophores in detail. They occur on the lower sides of the eyestalks, antennules and antennal scales, on the oral appendages, on the thoracic and abdominal sterna, on the ventral surface of the outer uropods, and on many of the leg joints. All are so situated that the light which they produce is thrown directly or obliquely downwards. In both the species photophores have been described on the lateral face of the carapace. These, however, at any rate in *S. challengerii*, are not external, but are placed in the roof of the branchial chamber and illuminate the gills from above (Pl. LIV. fig. 4). To find photophores in such a position as this is most astonishing, and it is not easy to suggest any theory which will account for their curious situation.

The photophores are all practically identical in structure and all are quite immovable, though a few are supported on very short, thick stalks in order to make them bear more directly downwards. They vary considerably in size, but even the largest are much smaller than the organs on the pleopods of *Acanthephyra debilis*. In a single individual the diameter of the lens was found to range from .06 to .14 mm.

The structure of the organs is illustrated in Pl. LIII. figs. 2-4 and in Pl. LIV. figs. 2, 3, & 5.

Externally there is a double convex lens. This is made up of two distinct portions, which are formed from the two layers composing the cuticle. The outer part is double convex, while the inner, which is closely applied to it, is concavo-convex. In sections treated with picro-carmin the inner lens often stains to a rather deeper red tone than the outer, but the complete absence of any yellow colour indicates that the cuticle of which both are formed

\* Hansen, P. Z. S. 1903, p. 72.

† Stebbing, Marine Invest. in S. Africa, vol. iv. 1905, p. 84.



is not more strongly chitinised than the rest of the exoskeleton. Both portions are quite transparent in material preserved in weak formalin. A very delicate investing membrane possibly occurs on the outer side of the lens, but its presence could not be demonstrated clearly in any of the sections obtained.

Situated immediately behind the lens and exceeding it in diameter is the first cellular layer. This is composed of a number of large wedge-shaped cells which appear to be derived from the epithelium; from eight to ten are seen in a median section of the organ. They are all full of protoplasm and their nuclei invariably lie close up against the lens. In material preserved in formalin this layer is seen to be impregnated with a deep blue pigment.

The second cellular layer is extremely inconspicuous; it consists merely of a few flattened nuclei round the outside of the first layer.

The third layer Hansen very reasonably considers to be a reflector. In material preserved in formalin it is of a distinctly yellow colour; it is faintly striated and contains numerous pear-shaped nuclei which are very regularly arranged with their narrow apices directed towards the lens.

The fourth and last layer consists of a number of irregularly disposed cells round the back of the reflector. It is possible that in life these carried a pigment, but in the preserved specimens no trace of this remains.

In some instances a nerve-strand communicating with the photophore was detected, but the exact mode of its entrance could not be discovered. It is not improbable that it runs round the edges of the reflector and then turns inwards to supply the first cellular layer, in much the same way as has been demonstrated by Chun in the photophores of Euphausians.

One of the two organs placed on the underside of the eyestalk is situated in closest proximity to the cornea. In this case (Pl. LIV. fig. 2) the photophore is slightly twisted and is directed forwards and downwards. It is shut off from the cornea by a layer of black pigment, and its nerve-supply is not drawn from any of the optic ganglia, but from a separate strand which runs up the inferior margin of the stalk.

It will be noticed from Pl. LIII. figs. 2, 3, that the lens may differ considerably in convexity, and in one case (fig. 4) it is plano-convex. This photophore is placed at the base of the exopod of the first maxillipede and is directed forwards; as Hansen mentions, it is partially, though not entirely, overlunged by the surrounding tissues.

In neither of the two species is anything known of the development. The photophores, however, differ slightly in number in the examples which I have examined, and it is probable that, as in the case of *Acanthephyra debilis*, they continue to increase as the specimen gains in size. Additional organs seem to appear long after the individual has attained maturity.

A comparison of the foregoing description with the account and figures which Hansen gives of the structure of these organs reveals many discrepancies. There can be little doubt that this is due to the fact that Hansen viewed the organs only in optical section, a method which, even in his hands, has not yielded satisfactory results.

#### THE PHOTOPHORES OF *ACANTHEPHYRA*.

Two species of *Acanthephyra* are known to possess photophores. They are first mentioned by Perrier in 1886\* in a form which he called "*Acanthephyra pellucida* A. Milne-Edwards." There is unfortunately a good deal of uncertainty regarding the validity of this species, for it has not been rediscovered in recent years and Milne-Edwards seems to have never published any description. Our knowledge of it is, in consequence, derived solely from the brief reference in Perrier's work, and the accuracy of the account of the distribution of the photophores, which is there given, is by no means certain†.

*Acanthephyra debilis* is better known. Coutière in 1905‡ first described the existence of photophores in this species, and in 1906§ he published a more complete account of their number and distribution.

The photophores in *A. debilis* are not all of similar structure, as they are in the case of *Sergestes*, but exist in different degrees of complexity in different parts of the animal.

The most highly developed organs are twelve in number, and each is so placed that the light which it produces is thrown directly downwards. One is situated on the distal and external aspect of the protopodite of each pleopod, and one behind the protopodite of each uropod. The structure of these photophores is illustrated in Pl. LII. fig. 1 and Pl. LIV. fig. 1.

Externally there is a thick concavo-convex || lens formed from the cuticle. In adult specimens this measures about .24 mm. in diameter, and during life is of a deep violet-blue colour. The pigment does not exist as a mere coating, but permeates throughout the structure of the lens. Sections stained with picrocarmine show that the lens is made up of three distinct layers. The inner and outer portions are merely thickenings of the two cuticular layers which form the normal exoskeleton of Crustacea and under a high power show the usual striations. The middle layer, which is also striated, always stains more deeply with carmine than the others, and, owing to the fact that it sometimes takes

\* Perrier, Les explorations sous-marines, 1886.

† A comparative view of the positions occupied by the photophores in *A. pellucida* and in *A. debilis* will be found in Kemp, Fisheries, Ireland, Sci. Invest., 1908, I. [1910], p. 67, where Perrier's original description is reprinted.

‡ Coutière, Bull. Mus. Océanog. Monaco, no. 48, 1905, p. 7.

§ Coutière, Bull. Mus. Océanog. Monaco, no. 70, 1906, p. 4.

|| In a few of the sections obtained the lens is plano-convex, but this I believe to be due to distortion.

up a certain amount of yellow colour (due to the picric acid in the stain), it seems probable that it is formed of a more strongly chitinated material. The cuticle is thrown in folds on either side of the lens. It is possible that by this structure a limited amount of movement is permitted to the photophore, but no trace of a controlling muscular apparatus could be found.

Inside the lens there is a series of very large elongate cells which radiate from a well-defined centre to its inner surface. They measure from .08 to .10 mm. in length; twenty are usually visible in a median longitudinal section, consequently at least three hundred must occur in the whole organ. The proximal portions of these cells appear to be wholly devoid of protoplasmal contents. The nuclei\* are very regular in shape and, as in the first cellular layer of *Sergestes*, lie close up against the lens. The outer end of each is evenly rounded, and a band of cytoplasm may sometimes be seen between it and the lens; the inner end is squarely truncate. The nuclei differ curiously in size, for in all the sections obtained the length is proportional to the distance from the centre of the lens. This results, in effect, in the formation of an additional lens, concavo-convex and built entirely of nuclei; which is placed immediately behind that formed from the cuticular layer. There can be little doubt that such a provision as this must have a marked effect on the optical qualities of the apparatus.

The central part of the organ is occupied by a number of minute highly refractive granules which are massed together in a conical shape round the extremity of the nerve-bundle. These granules are quite colourless in every section obtained; carmine, picric acid, and hæmatoxylin are all equally ineffectual in staining them. The nerve-strand leads straight down the pleopod to the photophore, and, as may be seen from the figures, it expands into a number of ramifying filaments before it converges to the granular cone.

Numerous cells with large nuclei are irregularly disposed round the inside of the photophore. It is possible that these were pigmented when the animal was living, and served as a screen to prevent light penetrating inwards, but no confirmation of this was obtained.

In a freshly caught specimen of *Acantheephyra debilis* a dark violet-blue streak is easily seen on each side of the inner wall of the carapace immediately behind the last pair of thoracic legs. From the structure which these organs possess it is evident that they also are photophores, although they are much less highly specialised than those at the base of the pleopods.

In a transverse section (Pl. LII. fig. 2) the lens, which is dark blue in fresh material, is seen to be merely a slight thickening of the cuticle, and the densely staining central layer is entirely absent. The epithelial cells are greatly elongated, as in the

\* There can be no doubt that these bodies are nuclei; for by the use of hæmatoxylin chromosomes were demonstrated in them.

photophores on the pleopods, but their arrangement is not so regular, and though the majority of the nuclei are placed near the lens this is by no means the case with all. The cells show a tendency to converge towards a point, but no granules similar to those in the other photophores were detected. In some sections a nerve-strand may be seen leading away from the organ and passing between two muscle-bands.

Other spots and streaks of dark blue pigment to the number of 133 are found in adult examples of *A. debilis*. They occur on the eyestalks, on certain legs, on the branchiostegites and other parts of the carapace, on the abdominal segments and on the telson. With the exception of a small number, which occur on the dorsal aspect of the carapace, abdomen and telson, all are situated laterally or ventrally.

Coutière, while fully realizing that little or no structural evidence could be advanced in favour of such a theory, has no hesitation in ascribing a luminous function to the cells underlying these pigment-spots. With this view I fully concur, and, as will be seen later on, I am able to bring forward another fact which supports this interpretation.

In the only passage in which he remarks on the anatomical characters of the organs, Coutière\* says: "Les organes lumineux de la base des pléopodes paraissent se rapprocher beaucoup de ceux des Euphausiæ, tous les autres semblent être de simples amas de cellules à lumière, disposées sur une seule assise et recouvertes de pigment." With the latter part of this sentence I am in entire agreement. In numerous sections, made through all the more prominent spots of pigment, the underlying cellular layer presents no visible difference from that of the adjacent tissue. To this there is only one exception: a section cut transversely through the telson near the apex (Pl. LIII. fig. 1) shows that the cells beneath the dorsal spot of pigment are greatly elongated, though their nuclei differ in position from those found in the more elaborate organs.

The brilliant scarlet-red pigment, which is such a notable characteristic of many deep-sea Decapods, presents features of special interest in the case of *Acantheephyra debilis*, for it is quite undeveloped in the neighbourhood of the luminous organs. This is particularly well shown in the case of the photophores at the base of the pleopods. Viewed laterally, these organs would be quite invisible, being wholly covered by the flaps formed by the abdominal pleura, were it not that in these parts the red pigment is entirely absent, leaving the transparent cuticle through which the light emitted by the photophore may shine as through a window. The luminous streaks behind the last pair of thoracic legs are covered by the branchiostegal wall of the carapace, and in these a precisely similar phenomenon may be observed.

Red pigment is also absent from the vicinity of all the numerous

\* *Loc. cit.* 1906, p. 4, footnote.

organs which, when sectioned, show no definite structure. In a freshly caught specimen each appears as a deep blue spot circumscribed by a belt of colourless tissue. Such a distribution of pigment seems to afford considerable support to the view, advanced by Coutière, that all the blue spots represent luminous organs.

An examination of young specimens of *A. debilis* shows that, as might have been expected, the complex organs are those which appear first. The eggs are very large and consequently the young are liberated in a rather advanced stage. The earliest-known larva possesses twelve luminous organs, viz., those on the pleopods and behind the fifth pair of legs. A little later the other compound photophores behind the protopodites of the uropods appear and simultaneously with them certain of the simple organs. At every succeeding moult fresh spots of blue pigment appear, until in the largest individual known they have reached the total of one hundred and forty-seven\*.

#### THE PHOTOPHORES OF *HOPLOPHORUS*.

Coutière (*loc. cit.* 1905, p. 1) first described these organs in a species which he named *Hoplophorus grimaldii*. Thanks to the kindness of Prof. Gardiner, I have been able to examine an example of this genus from the Indian Ocean. The specimen is unfortunately immature, but, as might have been expected, the photophores were not found to differ in any essential feature from those occurring in the closely related form *Acanthephyra debilis*. Although the simpler organs are by no means so numerous as in that species, all those of a more complex character are present and occur in the usual positions on the pleopods and uropods, and behind the base of the last pair of legs.

Coutière mentions that in his specimen of *Hoplophorus*, "conservé dans la glycérine formolée," the luminous organs are slightly yellowish; in the example from the Indian Ocean, which was preserved in spirit, no trace of pigment remains. The photophores are, however, so completely identical in structure with those occurring in *Acanthephyra*, that, notwithstanding the fact that the blue coloration has never been seen in *Hoplophorus*, there can be little doubt that such a pigment really exists in living specimens.

Whether the organs occur in all the species or whether, as in the case of *Sergestes* and *Acanthephyra*, they exist only in a limited number, must be left to future investigators.

#### THE PIGMENTATION OF THE PHOTOPHORES.

It has already been mentioned that a deep blue pigment is, in life, associated with the photophores of Decapoda, occurring in

\* For the order in which these organs arise and their number in specimens of different age, *v. Coutière, loc. cit.* 1906, and Kemp, Fisheries, Ireland, Sci. Invest., 1908, I. [1910].

*Sergestes* in the first cellular layer and in *Acanthephyra* in the lens itself.

There is reason to believe that this pigment is closely allied to, if not identical with, that found in the Lobster. When the photophore is placed in absolute alcohol the blue colour soon becomes bright red, and the same reaction instantaneously appears when it is boiled in a drop of water. If the lens of *Acanthephyra* be dissected out and treated with strong sulphuric or nitric acid the colour at once changes to red, and immediately afterwards turns to a dull greenish blue of a much less distinct colour than that originally present. The greenish-blue tone appears to fade away a little later, but the concluding stages of the reaction are somewhat obscured owing to the burning of the tissue by the acid.

The red pigment which gives the familiar colouring to *Nephrops* and to the lobster, when boiled, is known to be one of the lipochromes or fatty pigments, called by Moseley *crustaceorubin*, associated with a small quantity of yellow pigment, known as *hepatochrome*, which appears to be derived from the liver. The investigations of Krukenberg\* and of Miss Newbigin† seem to show that the unstable blue-black pigment or *lipochromogen* which occurs in the lobster is a compound of the red lipochrome with a complex organic base. The blue colour is turned red by any reagent which alters the form of the proteid, and the red pigment, extracted and dried, gives with strong acids a brilliant but evanescent blue reaction.

The photophores are unfortunately so minute that it is not possible to extract a solution of the pigment; but the reaction mentioned above, which was obtained by the addition of acid to the lens of *Acanthephyra*, furnishes fairly satisfactory evidence of the nature of the pigment‡. The acid breaks up the proteid and at once converts the blue *lipochromogen* into the red lipochrome, and this is immediately followed by the characteristic blue reaction which this pigment gives in the presence of an acid. The tissues burn and become brown under the influence of the reagent, and the rapid evanescence of the blue tint, which is characteristic in the case of dry extracted pigment, is in consequence somewhat masked.

It has not been possible to test the blue pigment in the photophores of *Sergestes* as fully as has been done in the case of

\* Krukenberg, Vergleich. Physiol. Studien, IIte Reihe, 3te Abteil., 1882, pp. 92-107.

† Newbigin, 'Journal of Physiology,' vol. xxi. 1897, p. 237.

‡ The following observations on the red colouring-matter of *Acanthephyra* may be mentioned here. An ether extract of the pigment gave a bright yellow solution, which on evaporation yielded an oily red extract. On the addition of strong nitric acid a bright, but rapidly evanescent, blue reaction was obtained which was followed by the separation of the red matter from the oily yellow pigment, the latter turning a dull green. This result is practically identical with that obtained by Miss Newbigin with the extracted pigments of *Nephrops*. The red colouring which turns blue under the influence of the acid is the lipochrome, *crustaceorubin*, while the oily yellow pigment is *hepatochrome*.

*Acanthephyra*, but from the fact that it turns red when boiled or when treated with strong acids it is very probable that it is of the same nature.

The existence of blue coloration in deep-sea animals is exceedingly rare, and its occurrence among Decapoda in close association with the photophores is almost unique, for among the Euphausiacea a similar pigment appears to have been noticed only on a single occasion. In November, 1909, a large specimen of *Thysanopoda acutifrons* Holt & Tattersall was caught in a mid-water net off the West coast of Ireland. This specimen, which was dead by the time it reached the deck, was found to possess patches of deep blue pigment associated with the photophores on the eyestalks. Casual examination failed to reveal this pigment in the other photophores, which, however, were of a darker colour than is usually the case. The specimen was put aside in a dish of water and when it was again examined, not more than half an hour later, all trace of the blue pigment had vanished. It is evident that, even if in this case the blue colouring invariably occurs in the photophores, the phenomenon is one of great rarity among Euphausians, for it certainly is not found in *Meganyctiphanes norvegica* or in any of the common N. Atlantic species.

The blue pigment of the photophores of Decapoda is much more stable than that noticed in *T. acutifrons*. Although rapidly extracted by alcohol, it will persist for years in specimens preserved in weak formalin, remaining distinct long after the general red colouring has disappeared.

The lens of *Acanthephyra*, being blue, can necessarily only allow the emission of blue light and it is not impossible that this is also true in the case of *Sergestes*, where the lens is transparent and the first cellular layer blue. It seems then that, at least in the former genus, the production of blue light is a necessity, but it is impossible to suggest any explanation of this curious phenomenon.

Photophores have evidently been developed by Crustacea in at least three separate instances. Those possessed by *Acanthephyra* and *Hoplophorus* are in structure wholly distinct from those of *Sergestes*, while in neither case is there any resemblance to the very complex organs of the Euphausiacea.

It is a remarkable fact that, whereas in the latter order the possession of photophores is the general rule (only in *Bentheuphausia* are they absent), their occurrence in large genera such as *Sergestes* and *Acanthephyra* is limited to a few species only. This is particularly noteworthy in *Sergestes*, in which two forms, both of which are classed among a small group of extremely closely allied species, exhibit a large number of photophores, whereas none are to be found in the other members composing the group.

Doflein, in a short but interesting paper \*, has summarised the

\* Doflein, Sitzungsber. d. Ges. f. Morphol. und Physiol. in München, xxii. 1907, pp. 133-136.

various suggestions which have been made as to the use of luminous organs to marine animals. He remarks that they probably serve different functions in different groups of animals and classes them in four sections.

i. Attraction of prey (chiefly important in sessile or slowly moving animals).

ii. Attraction of other individuals of the same species, either (a) for the formation and maintenance of swarms or (b) to enable the sexes to find and recognise one another. In this connection Doflein points out that animals with a complicated system of photophores always possess highly developed eyes, and refers to Brauer's theory that the varying arrangement of photophores produces light patterns serving as recognition marks, like the colour-patterns of animals living in daylight.

iii. Protection. The clouds of luminous secretion emitted by some species may possibly serve the same purpose as the ink of the cuttlefish, and photophores may also by a sudden flash of light scare a pursuer. In the fauna of land and shallow water a brilliant colouring is often assumed as a signal that the species is distasteful, and some deep-sea animals may, for the same purpose, exhibit warning lights.

iv. Illumination of objects viewed by the animal. On this theory it is difficult to account for the ventral and lateral position of the photophores in many marine animals\*. In Crustacea this is particularly well shown, for the large majority of the organs illuminate regions which seem altogether out of range of the eyesight.

It is evident that these suggestions will not account for every case which can be found; the photophores in the roof of the branchial chamber of *Sergestes* remain inexplicable.

The vast majority of marine animals which possess photophores live at the surface or at intermediate depths and never occur on the bottom. No exceptions to this rule have been noticed in the deep-water fauna of the Irish Atlantic slope, but it seems that the two Euphausians, *Meganyctiphanes norvegica* and *Nyctiphanes couchii*, are sometimes found on the bottom in shallow water. On one or two occasions large numbers of these two species have been caught off the Irish coast at depths of 40 to 60 fathoms, and there are indications that the specimens which were obtained in these hauls were actually living on the sea-floor. The same two species are frequently obtained over depths of 400-800 fathoms off the West coast of Ireland, and here they invariably occur in midwater.

It must be remembered that the ordinary open-mouthed nets, which are generally employed for bottom work, frequently catch

\* Miss Massey informs me that when studying the development of the Cephalopod, *Histioteuthis bonelliana*, which when adult possesses photophores all round its body, she noticed that the organs are developed first on the side which is ventral when the animal is swimming.



midwater organisms while being hauled, and there is reason to believe that errors arising from this source exist in many of the instances in which animals bearing photophores have been recorded from the bottom.

Many of the higher marine animals live on the sea-floor at depths to which no ray of sunlight can ever penetrate, and, though they possess well-developed eyes, are themselves, for the most part, without any special illuminating apparatus. That light exists at these depths seems almost certain. It is probably fairly plentiful in regions thickly populated by Cœlenterates, and the excretions of numerous animals of a more highly organised nature have been found to be brilliantly phosphorescent. The restriction of photophores to species living in midwater seems only explicable on the theory that there is a comparatively plentiful supply of light on the bottom itself.

The sections of the photophores were made by the paraffin method in the laboratories of Trinity College, Dublin. Decalcification was not attempted, for it was found that the cuticle was sufficiently soft without it, this, perhaps, being due to the fact that the specimens were preserved in formalin.

In conclusion, I wish to acknowledge my indebtedness to Dr. W. T. Calman for much useful help and criticism, and to Dr. H. H. Dixon for his valuable assistance and advice in the preparation of the sections and micro-photographs.

#### EXPLANATION OF THE PLATES.

##### PLATE LII.

The figures on this Plate are reproduced from micro-photographs.

##### *Acanthephyra debilis* A. M.-Edw.

- Fig. 1. A longitudinal section of a photophore from the protopodite of the pleopod.  $\times 185$ . (Compare fig. 1, Pl. LIV.)  
2. A transverse section of the photophore behind the base of the last pair of legs.  $\times 133$ .

##### PLATE LIII.

The figures on this Plate are reproduced from micro-photographs.

##### *Acanthephyra debilis* A. M.-Edw.

- Fig. 1. A transverse section of the telson near the apex, passing through the median dorsal patch of blue pigment. The section shows the regular arrangement of nuclei below this area and also the bases of two spines cut transversely.  $\times 93$ .

##### *Sergestes challengerii* Hansen.

- Fig. 2. A median photophore from the thoracic sternum, cut transversely.  $\times 320$ .  
3. Part of the penultimate joint of the second maxillipede, cut longitudinally, showing a photophore in transverse section.  $\times 247$ . (Compare fig. 3, Pl. LIV.)  
4. The photophore at the base of the exopod of the first maxillipede in transverse section.  $\times 300$ .

## PLATE LIV.

The figures on this Plate are semi-diagrammatic.

*Acanthephyra debilis* A. M.-Edw.

Fig. 1. A longitudinal section of a photophore from the propodite of a pleopod. The cellular layer (*c.*), which is apparently derived from the epithelium, is composed of long cells with densely staining nuclei at their outer ends. The only cytoplasm which is visible lies between the nuclei and the inner face of the lens.  $\times 210$ . (Compare fig. 1, Pl. LII.)

*Sergestes challengerii* Hansen.

Fig. 2. A longitudinal section of the eye-stalk showing the photophore (*ph.*) lying close to the eye (*e.*) and separated from it by a curtain of black pigment (*p.*).  $\times 160$ .

3. A photophore from the penultimate joint of the second maxillipede in transverse section.  $\times 380$ . (Compare fig. 3, Pl. LIII.)

4. A transverse section of the branchial chamber showing an arthrobranch (*a.*) and one of the four photophores (*ph.*) which are set in the roof of the cavity and appear to illuminate the gills from above.  $\times 44$ .

5. The same photophore on a larger scale. The two layers of the lens (*i.l.* and *o.l.*) and the first cellular layer (*c.*) are formed from the cuticular and epithelial layers of the inner surface of the branchiostegite.  $\times 380$ .

## Reference letters :—

- a.* Arthrobranch.
- b.* Branchiostegite.
- c.* Cellular layer (in *Acanthephyra*.)
- c'*. First cellular layer (in *Sergestes*.)
- c''*. Second cellular layer (in *Sergestes*.)
- e.* Eye.
- e.l.* Epithelial cell-layer.
- g.* Cone of minute highly refractive granules in close connection with nerve-strand.
- i.e.* Inner cuticular layer of branchiostegite.

- i.l.* Inner layer of lens.
- m.l.* Middle layer of lens.
- n.* Nerve.
- o.* Optic ganglia.
- o.c.* Outer cuticular layer of branchiostegite.
- o.l.* Outer layer of lens.
- p.* Curtain of black pigment between photophore and eye.
- ph.* Photophore.
- r.* Reflector or striated layer.
- s.l.* Sheathing layer of cells.

## 2. On the Varieties of *Mus rattus* in Egypt; with General Notes on the Species having reference to Variation and Heredity. By J. LEWIS BONHOTE, M.A., F.L.S., F.Z.S.

[Received December 22, 1909.]

(Text-figures 58-62.)

While spending a few months recently at the Giza Zoological Gardens, near Cairo, I was enabled through the kindness of the Director, Capt. S. S. Flower, to examine a large number of the common House Rats of the district. I gladly took advantage of the opportunities thus offered, as I was convinced that a close study of this species would throw some light both on the causes of variation and on the inheritance of the varieties that are found in such profusion in *Mus rattus*.

In addition to the rats which were caught in the Gardens, Dr. Charles Todd, of the Public Health Department, kindly allowed me to examine and measure all the rats that came into his hands during the time that I was in Cairo. These rats were taken in various towns and villages in the Delta by special catchers employed by the Public Health Department, the result being that

criticised my paper and comes to the conclusion that my effort has not cleared up the confusion and that all these rats belong to one and the same species—*Mus rattus*.

Dr. Hossack's remarks, fair and just as they appear to be, fail from the fact that we were working at the subject from entirely different points of view—he as a medical man, anxious to know the number of species by which the plague might be conveyed—I, as a zoologist, seeking for a law and order in the apparently innumerable varieties found among these rats. For Dr. Hossack's purpose it is sufficient to know that there are but two species of true rats, usually found in houses—the short-tailed, heavy-built and practically invariable *Mus norvegicus*, and the long, slender, and extremely variable *Mus rattus*, which includes *all* the varieties bearing the mass of names that so confused my critic. Had he written to me in the first place, I could have told him at once that all these long-tailed rats belonged to one very variable species, and that in the large towns, where all his material was procured, no order or classification was possible as the varieties had become hopelessly mixed and crossed, but that in the country places the varieties were much better defined, and apparently bred true. The question of the classification and study of these varieties is a specialised study for zoologists, and it is not to be expected that a medical man, studying the plague, should be able to devote the time necessary for the thrashing out of such matters.

It would therefore have been better had he applied to recognised authorities for his information, rather than attempt a task in a specialised subject outside the scope of his investigations.

I am glad to have had this opportunity of replying to Dr. Hossack, for many people do not yet realize that the study of geographical forms and minute variations has a very great bearing on many large and important zoological problems, but need not concern the man engaged on other cognate investigations, and in the present instance it is sufficient for him to know that all these varieties of the long-tailed rat belong to one species, *Mus rattus*.

#### *Mus rattus in Egypt.*

In Egypt we find two distinct forms of *Mus rattus*—the one with pure white underparts and white feet, which was named *Mus tectorum*\* by Savi; and the other with slate-grey underparts and dark feet, which may be known as *Mus alexandrinus*†. Between these two forms many intermediates occur, the actual typical forms being comparatively rare‡.

\* *Mus tectorum* Savi, Nuovo Giorn. Pisa, 1825.

† *Mus alexandrinus* Geoff. Descr. de l'Egypte, Hist. Nat. ii. p. 733; Atlas, pl. v. fig. 1 (1812).

‡ This statement apparently contradicts the remarks on p. 653, but it must be borne in mind that those remarks were based on Malay material, obtained in centres removed from the influence of foreign shipping, whereas in the present case the specimens came from populous centres, contiguous to a large waterway (the Nile and its branches).

I have already referred to the fact that in India the three varieties of *M. rattus* may roughly be considered as hill, tree, and house forms; but in Egypt, where the cultivated parts frequented by these rats are low-lying and level plains, only two forms were found.

I made a number of careful observations in the Giza Gardens, where both forms are found, to see whether the two varieties were really different in their habits; but such evidence as I was able to get together was very inconclusive. Large numbers of plane trees grow in the Gardens and on these, often at a considerable height from the ground, many heaps of the fruit, looking not unlike squirrels' dreys, were to be found. These were undoubtedly brought together by rats, but investigation proved that they were used merely as convenient platforms on which to feed, and *not* as sleeping or breeding places. The seeds of these trees are apparently a favourite food, and as it would be impossible for a rat to devour them *in situ*, they are picked and carried to the first convenient spot, generally a fork near the main trunk, to be devoured, and it is on such places that the accumulated débris forms the apparent nests. On the other hand, the fruit which had fallen to the ground was frequently taken into a neighbouring bush and eaten there, so that there is undoubtedly a tendency to an arboreal life.

On two occasions only did I actually see a rat in a tree, and neither time were they accurately identified, although one, I am almost certain, belonged to the white-bellied form (*M. tectorum*). Both forms were found living in burrows in the ground as well as in the houses, so that there seems to be but little difference in habits between the two varieties. The apparent absence of the third (Indian) subgroup, however, taken in correlation with the lack of high ground, seems certainly suggestive, but I shall have more to say on this point later.

In studying the various forms of *Mus rattus* I found it convenient to classify them into four groups.

- (i.) *The Typical Tectorum*, in which the hairs of the underparts are white to their bases and the upper surface of the hind feet is also white.
- (ii.) *The Grey Tectorum*, in which the hairs of the underparts are white to their bases but the upper surface of the hind feet shows traces of brown.
- (iii.) *The Grey Alexandrinus*, in which the hairs of the underparts have slate-coloured bases and the upper surface of the hind feet shows much brown.
- (iv.) *The Typical Alexandrinus*, in which the hairs of the underparts are slate-coloured throughout or nearly so, and the hind feet entirely brown on the upper surface.

In actual shade of colour much variation was shown. Groups (iii.) and (iv.) were constantly darker than groups (i.) and (ii.).

but in classifying them, reliance was only placed on the characters noted above, which allowed no possibility of doubt.

[*Mus norvegicus*, on the other hand, proved very constant and no variation in colour was noticeable. In this species, the hairs of the underparts have slate-grey bases and the upper surface of the hind feet is pure white, a combination of characters apparently not found in *M. rattus* from Egypt.

Apart from this distinction, *M. norvegicus* is a larger and more stoutly built animal; the length of the tail *never* exceeds that of the head and body, and the ears are shorter and more rounded. There are also some easily recognisable skull differences, which need not be gone into here.]

Every specimen was carefully measured in the flesh by myself with the same callipers, so that errors from a comparison of measurements are reduced to a minimum. The measurements taken were: snout to root of tail, tail, hind foot, ear.

The largest measurements in mm. were as follows:—

		Head & body.	Tail.	Ear.	Hind foot.
<i>Mus norvegicus</i> .	♂ ad. No. 250 ...	253	233	22	43
" "	♀ ad. No. 215 ...	225	204	19	41
<i>Mus r. tectorum</i> .	♂ ad. No. 203 ...	188	232	24	35.5
" "	♀ ad. No. 181 ...	190	232	24	36.5
<i>Mus r. alexandrinus</i> .	♂ ad. No. 290 ...	199	220	26	35
" "	♀ ad. No. 287 ...	195	208	26	35

[These measurements are given only as showing the greatest sizes attained; they are those of individuals and in no sense average measurements, so that, for instance, it must not be assumed that the ears of *M. alexandrinus* are on the average larger than those of *M. tectorum*. Owing to the difficulty of accurately estimating the age of any individual, it is impossible to give average measurements.]

The proportionate lengths of the body and tail measurements were found to vary in both species, but in *M. norvegicus* the tail never exceeded the body length, and in *M. rattus* the tail was always longer than the body length.

The most reliable measurement therefore on which to make comparisons and the only one which dealt with a structural feature and for that reason admitted of least error, was that of the hind foot. This measurement may therefore be taken as a fair criterion of general size and as forming a good and reliable index for comparison.

Curves of this measurement were made, and on referring to that of *Mus rattus* (Table I., text-fig. 58), we note that the male

Text-fig. 58.

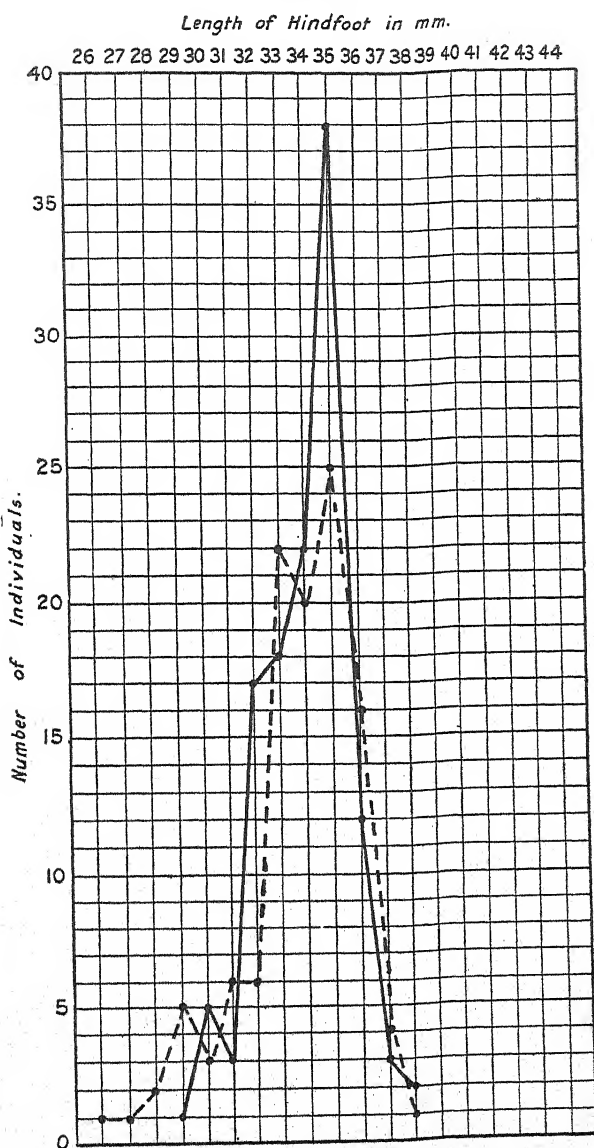


TABLE I.

Curve of hind-foot measurements of *Mus rattus* (all forms).  
 The dotted line represents measurements of the males.

curve (dotted line) shows three apices at 29, 33, and 35 mm., and that the female curve shows an apex at 30 and 35 with a break in continuity between 32 and 34; that is to say, both sexes show three apices, and that therefore a larger number of rats have hind feet of those three measurements than of the intervening sizes. Now, as these measurements include rats of all ages, and as there is no reason why there should be more of one particular age than another, seeing that the breeding season is fairly continuous throughout the year, it follows that we have here three 'limits of growth,' or, in other words, that certain individuals reach their limit of size at these three points, and consequently that the numbers at these points tend to accumulate and thus to form the apices in the curve. Those who accept Mendel's theory would here maintain, and probably with justice, that each apex represents a mutation, and that around these mutations fluctuating variations would occur so that, unless closely examined, the whole series would appear as a case of continuous variation.

Text-fig. 59.

*Length of Hindfoot in mm.*

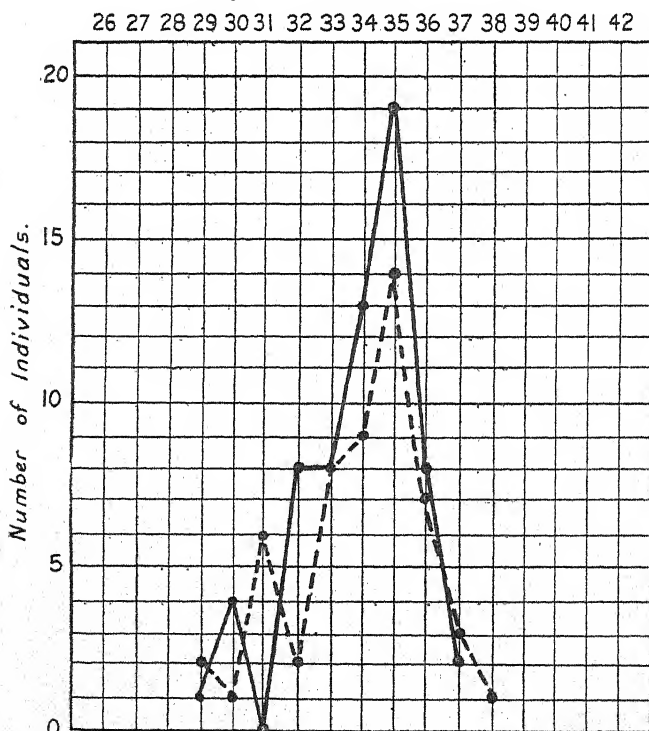


TABLE II.

Curve of hind-foot measurements of *Mus rattus tectorum* [Groups i. & ii.].

Text-fig. 60.

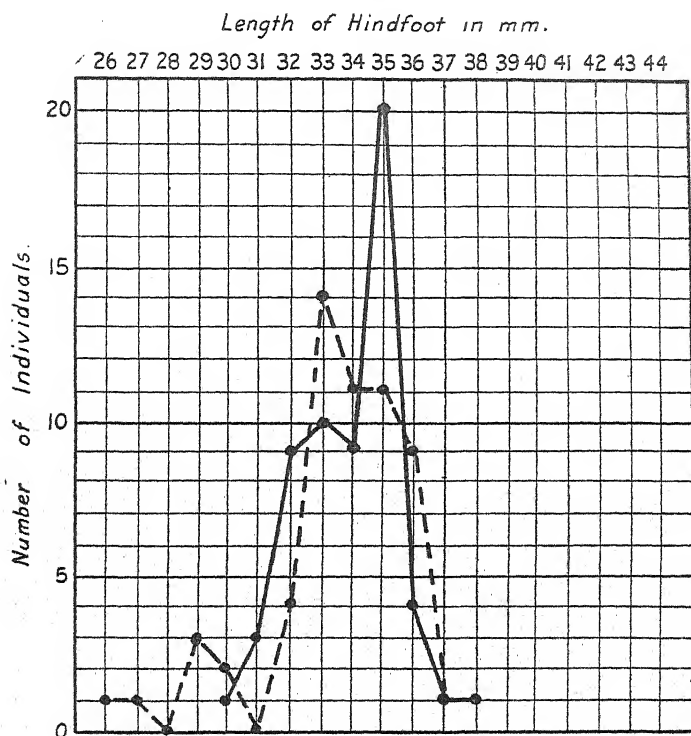


TABLE III.

Curve of hind-foot measurements of *Mus rattus alexandrinus* [Groups iii. & iv.].

(N.B.—Tables II. &amp; III. are represented together in Table I.)

Tables II. and III. (text-figs. 59 & 60) show the curves of *M. r. tectorum* and *M. r. alexandrinus* taken separately. In the first table I have included all the rats which would fall under groups (i.) and (ii.), and in the second those included in groups (iii.) and (iv.) (see *ante*, p. 655).

The *tectorum* males show apices at 31 and 35 mm. with a slight check at 33, and the females at 30 and 35 with a slight check at 32-33. In *alexandrinus* the males show apices at 29 and 33 with a slight check at 35, and the females a slight apex at 33 with a large one at 35. There were no females of *alexandrinus* below 30, which accounts for the absence of the first apex.

This comparison makes it very clear that the apices in the general curve (Table I., text-fig. 58, p. 657) are not merely due to accident, but that the middle one at 33 represents the variety known as *alexandrinus*, and the largest one at 35 represents the white-bellied *tectorum*. The fact of the curves in Tables II.



and III. showing traces of the other apices, does not invalidate the reasoning as groups (ii.) and (iii.) are intermediate forms.

### Mus rattus.

#### *Comparison of Indian and Egyptian Forms.*

The next question to arise is, what is the significance of the third and smallest apex at 29 and 30 mm. On reference to my paper quoted above in which I had divided *M. rattus* into three subgroups, we find the hind-foot measurements as follows:—

<i>Jalorensis</i>	subgroup,	hill form.	Hind foot	30 mm. (29–31·5).
<i>Rufescens</i>	„	tree form.	„	33 mm.
<i>Griseiventer</i>	„	house form.	„	35 mm.

These measurements, it will be noted, correspond exactly to the three apices in the curves of the Egyptian rats; so that we are, I think, justified in considering the small apex at 29 to represent the hill form (*Jalorensis* subgroup) of the Oriental Region, but which has become, in the level country of Egypt, unrecognisable externally.

This is a point which is of extreme importance from a deeper and more general point of view, for here, in a low-lying country, we have traces of a variety which in another part of the world has become the predominant form in the hills. Now, if continuous variation were the only method of evolution, we should find that in a level country all variations suitable to the hills would be eliminated, so that, in course of years, no trace of them would remain as they would be swamped by the more suitable forms, but apparently this has not happened in the present instance. The small-footed variety is still present in Egypt, permeating the race, and still existing in sufficiently strong numbers to spring up again quickly and become a dominant form should it ever find itself under suitable conditions.

Although, perhaps, not absolutely conclusive, this affords considerable evidence that the three subgroups of *M. rattus*, which I first differentiated in 1903 and which are strongly confirmed by the present work, probably arose as mutations.

There is yet a further point. One of the characters of the *Jalorensis* subgroup (the hill form) is the pure white hairs of the underparts. In this case it is associated with a small hind foot, but in Egypt we find it in *M. tectorum*, which has the largest hind foot of the three forms. It is therefore evident that the colour of the underparts is a character which has not always been inherited in connection with the size of the foot, but may occur in any one of the subgroups, so that in one country it may be characteristic of the hill form, in another of the tree form, and so on\*.

\* I am aware that on the evidence so far brought forward it might be argued that, if the colour of the underparts is not always found in correlation with the same sized hind foot, it is a character of but little use in distinguishing the sub-

*Comparison of M. rattus and M. norvegicus.*

Passing now from *M. rattus* to *M. norvegicus* and comparing Tables I. (text-fig. 58, p. 657) and IV. (text-fig. 61), we find a striking and surprising analogy in the curves. As in the case

Text-fig. 61.

*Length of Hindfoot in mm.*

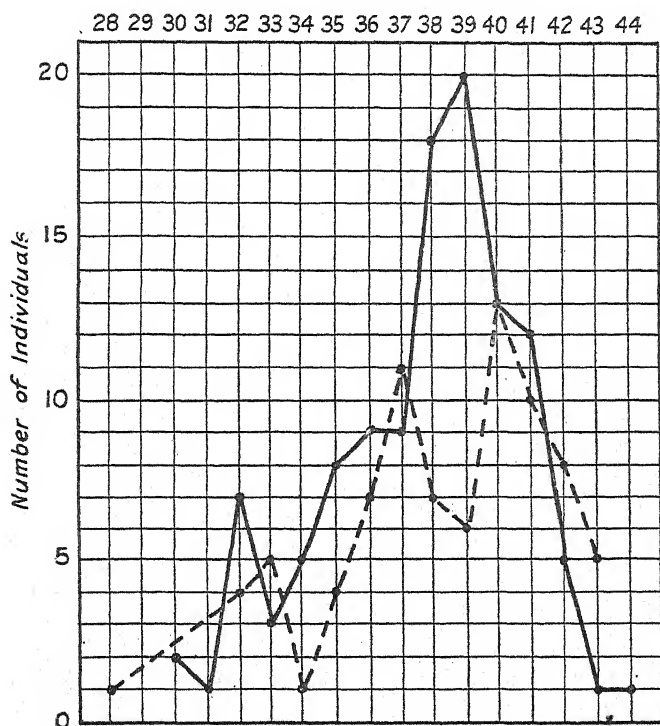


TABLE IV.

Curve of hind-foot measurements of *Mus norvegicus*.

of *M. rattus*, *M. norvegicus* also shows three apices at 32, 37, and 39, but in this case there is no colour variation, and therefore no

groups, for being a separate mutation it might be found (if the hind-foot measurement were taken as the determinant character of the subgroup) in two or more of the subgroups.

The answer to this objection according to our *present* knowledge is that in any particular locality we have always found it associated with one, and *only one*, size of hind foot; that is to say, always in the same subgroup as defined by the size of the foot. Furthermore the breeding experiments, so far as they have gone, seem to point to the fact that it *is* inherited in correlation with the size of the hind foot in the rats from Egypt.

means of individually distinguishing the different forms or mutations, as we may now, I think, call them.

Here, therefore, in an entirely different species we find the same mutations present, and whereas in the case of the one (*M. rattus*) we are enabled to distinguish easily the various forms owing to the combination of the hind-foot character with a colour character, yet in the other species (*M. norvegicus*) we are unable to subdivide it into three forms, owing to the impossibility of definitely detecting which character is present in any particular individual. Nevertheless we have cognisance of characters (mutations) which cannot be recognised by any external inspection of individuals, although we have proved their presence beyond a doubt.

It would of course be rash to be too positive, yet it is extremely unlikely that these rats tend in any way to pair according to their foot character. If the characters were therefore merely individual variations, they would undoubtedly tend to be swamped and an even curve would result. This, however, is not the case. [For purposes of comparison we have added (Table V., text-fig. 62) a curve of the hind foot of *Acomys calvirinus*; this, it will be noted, is a perfectly simple curve with only one apex. As the number of *Acomys* measured (about 100) was nearly the same as the number of *M. alexandrinus*, the comparison is a perfectly fair one.]

We have here, therefore, in *M. norvegicus* a splendid example of a Mendelian character (mutation) being carried on unpaired through generations; and there can be little doubt that if these animals found themselves under certain conditions where small feet, for example, prove of great advantage, very few generations would suffice for the small-footed race to become the dominant form.

The Mendelian theory enables us to understand how a small-footed race could be produced in a very short time, or how, if that favourable mutation were not present, the species might die out before the cumulative effects of Natural Selection on continuous variation would have time to act.

#### General Notes.

Much work of value still remains to be done by enquiry into the gradual formation of species, and these rats offer a wide field for the study of minute variations. Many groups of the smaller rodents as, for example, rats of the *Mus jerdoni* group and many of the Oriental groups of squirrels, offer similar problems of great complexity. In the former case we have numbers of very closely allied forms all inhabiting the same district, and each form has, apparently, its representative in other neighbouring districts. Systematists of late years have been content to burden each of these forms with a different name and there to leave the matter. Such work, necessary as it may be, can be but a preliminary step, and unless the subject is pursued further, the chaos

brought about by a multitude of names is worse than the old plan by which one name was made to cover all varieties.

More recently still, the rediscovery of Mendel's theory has, at

Text-fig. 62.

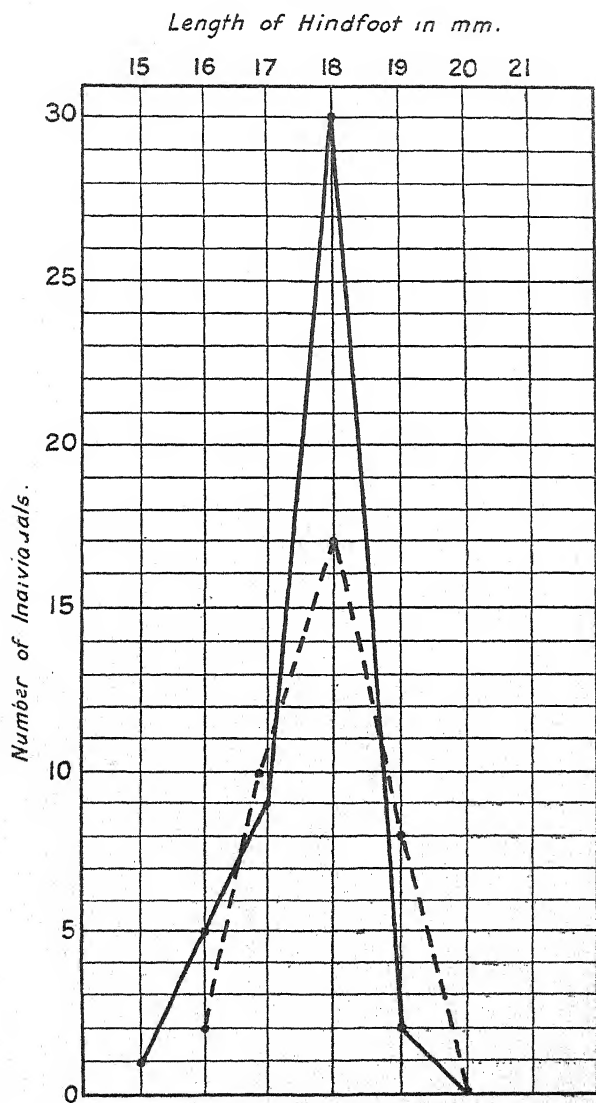


TABLE V.

Curve of hind-foot measurements of *Acomys cahirinus*, to show simple curve for comparison with previous Tables.

least, given a working hypothesis on which we may attempt to solve some of the problems of heredity; and though I am far from admitting that Mendel's law is the sole, or even the chief, factor governing heredity, it does undoubtedly help us to understand how these closely allied forms can either (i.) exist in the same locality as distinct varieties, or (ii.) in another locality become apparently lost although a closer inspection shows them to be present, only waiting for a suitable environment in which to develope.

To prove this matter further, it becomes necessary to conduct Mendelian experiments on these varieties. This I have begun to do on a small scale. The experiments are, however, as yet in the initial stages and no definite results can be stated. So far as they have gone, we find that pure *M. tectorum* mated with pure *M. tectorum* have produced pure *M. tectorum*. Pure *M. alexandrinus* when paired together have also bred absolutely true. A pair of grey *M. tectorum* (group ii.) showing slight traces of brown on the feet produced young like themselves (group ii.) and grey *M. alexandrinus* (group iii.).

As far as it goes, therefore, this evidence seems to further confirm the fact that *Mus rattus* should not be regarded as a species in which variation has run wild, but rather as a species containing certain definite mutations, which when mated together breed perfectly true. From its wandering habits and prolific breeding much intercrossing takes place, giving rise to these innumerable varieties, but no better evidence could be had of the purity of the gametes than the fact that when the apparently pure races are mated together (even when captured amongst a mixed crowd) they breed absolutely true.

#### Summary.

The main points that have been brought out in this paper are as follows:—

(i.) Two varieties (and intermediates) of *M. rattus* are found in Egypt.

(ii.) The hind foot is taken as a standard measurement and curves of this measurement drawn.

(iii.) These curves show three apices, the first being very small.

(iv.) These three apices correspond with the length of the hind foot typical of the three subgroups of *M. rattus* in the Oriental Region described by myself some years ago.

(v.) Hence it is argued that these three apices probably represent mutations, and that the first and smallest apex represents the *Jalorensis* subgroup found in the Oriental Region, but which from some cause or other is practically non-existent in Egypt.

Since, however, a mutation cannot be destroyed, we still find it in a small percentage of individuals ready under favourable circumstances to increase.

It is pointed out that this may account for the very quick way in which some species accommodate themselves to altered surroundings, since if a favourable mutation is present in the species very few generations would suffice to make it the dominant form.

(vi.) In *M. rattus* we found that the length of the hind foot was also correlated with external differences, and that the white-bellied *M. tectorum* had a longer hind foot than the darker *M. alexandrinus*.

Although in the Oriental Region the pure white underparts is characteristic of one of the subgroups, yet in that region it is correlated with a different sized hind foot to that with which it is associated in Egypt. Therefore the length of the hind foot and the colour of the underparts, although both pure mutations, can probably be inherited independently.

(vii.) An examination of the hind-foot curve in *M. norvegicus* shows also three apices, but in this case there is no colour-character by which the mutations may be distinguished externally. The length of the hind foot as a mutation is therefore a character common to two or more species.

(viii.) It is suggested that this enables us to understand how several very nearly allied forms of the same species (e. g. in *Mus jerdoni* and some of the *Sciuridae*) may exist in the same locality without losing their characteristic differences, however small those differences may be.

(ix.) Further investigation on these lines is required by means of experiments in heredity, and so far as the author has carried these out the pure varieties of *M. tectorum* and *M. alexandrinus* were found to breed perfectly true.

(x.) Lastly, this paper claims to show that *Mus rattus* is a species containing many slight but definite mutations which, as far as the evidence goes, breed true when paired together, and that the apparent innumerable and indefinite variations are merely due to these animals being carried all over the world and mixing together in the large seaport towns.

In short:—The varieties in *Mus rattus* appear to run on definite lines and to have arisen as mutations, they are therefore inherited on Mendelian lines. Of the three main varieties found in the Oriental Region only two occur in Egypt, but this paper shows the presence of the third, though in very small numbers. One of the characters of these varieties is shown to be present in another species, *M. norvegicus*, although it cannot be distinguished in any particular individual. It is further hinted that many of these so-called species which are very closely allied have probably arisen as mutations, and that it is due to this fact that they are able to exist side by side under precisely the same conditions and yet preserve their characters intact. It may also be noticed that the colour-character of the hairs on the underparts is also found in another species, namely, the house-mouse, *Mus musculus*. *M. m. gentilis* has the hairs white to their bases, while *M. m. orientalis* has slate-coloured bases. Both these forms occur in Egypt.

3. On an example of Posterior Dichotomy in an Aylesbury Duckling. By G. E. BULLEN.\*

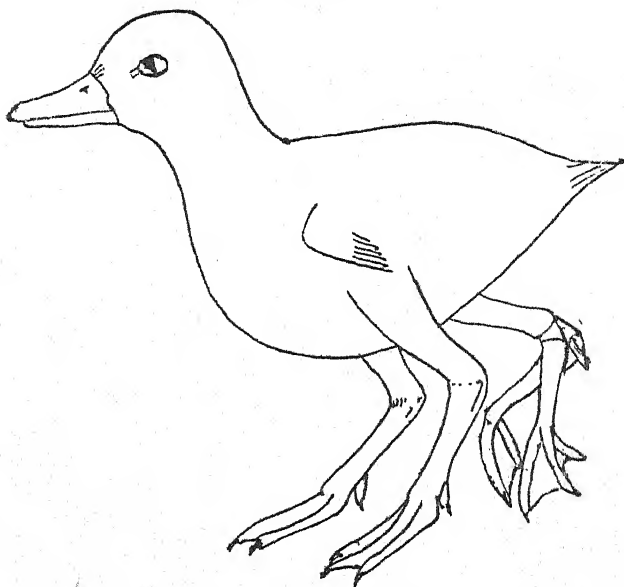
[Received March 14, 1910.]

(Text-figures 63 & 64.)

It is well known that instances of dichotomy and the reduplication of limbs occur not unfrequently in domesticated mammals and birds. Many examples of such malformations have been recorded hitherto by such authors as Förster, St. Hilaire, Allfeld, Albers, Ballantyne, His, and Bland Sutton.

The last named, in his work entitled 'Evolution and Disease,' describes amongst other examples of birds having supernumerary pelvic and other limbs, a chick, which presents the most frequently observed characters of posterior dichotomy. In the main, the subject of the present paper is somewhat similar, but with the addition of certain well-marked deviating characters which do not appear to have been described by any previous author.

Text-fig. 63.



Aylesbury Duckling, with supernumerary legs (reduced).

The specimen under discussion (text-fig. 63), now in the

\* Communicated by JOHN HOPKINSON, F.L.S., F.Z.S.

Hertfordshire County Museum, was hatched in July 1909, and lived for about twenty-four hours. There appear to have been

Text-fig. 64.

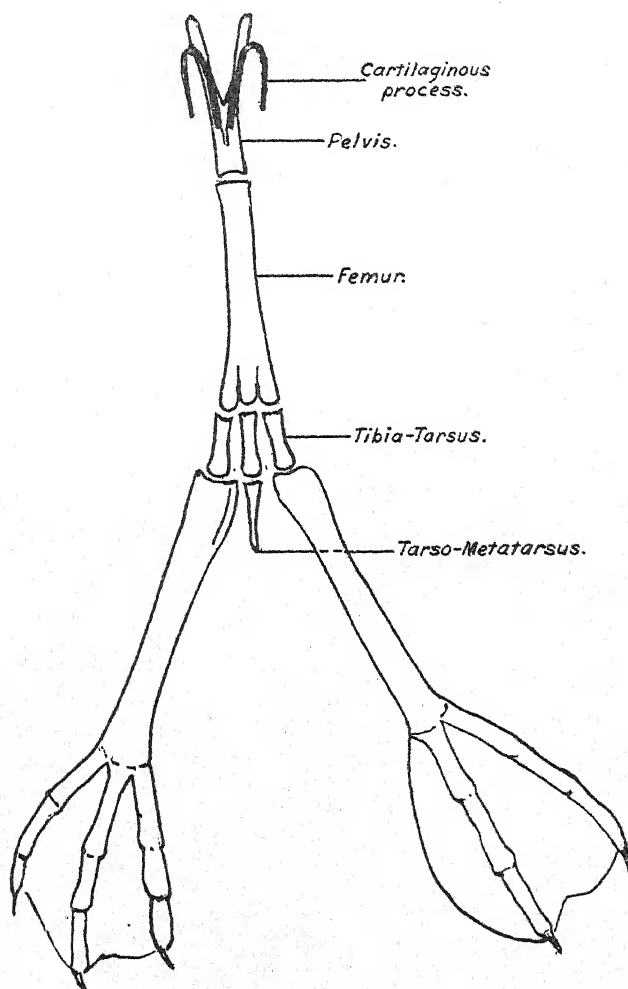


Diagram showing form and relative position of bones composing supernumerary legs (twice enlarged).

two individuals with supernumerary legs from the same batch of eggs, but the second specimen did not pass into the author's



hands. It was stated that the autosite, in both instances, had no control over the supernumerary legs.

Briefly to summarise the result of the dissection, the following features were found to exist in the part dichotomised, which occupied a median position on the ventral aspect, and, as usual in such cases, was stunted generally in growth. The pelvis was reduplicated and malformed; the femora were fused together, and supported *three*, and not two stunted, tibiae. The fibulae and patellae were entirely absent. The two outside limbs were further well-developed as described later, whereas the third limb holding a median position on the base of the confluent femur terminated with a tarso-metatarsus, reduced to a mere spike-like projection, covered, however, with scaly integument.

The reduplicated pelvis did not appear to be attached in any way to the body of the autosite, but was contained entirely within the integument. Its form, as shown in the illustration (text-fig. 64), would appear to suggest a tendency toward atavistic structure, embodying as it does certain characters seen in the iliac arch of Batrachians.

The writer desires merely to place the fact of this apparent similarity before the reader, without throwing any particular stress upon it, for as Gegenbaur has insisted, and his opinion has been backed by subsequent investigators, atavism cannot be accepted as an explanation of resemblances between forms that are systematically far distant. It is generally found that striking instances of supposed atavism are the result of misinterpretation.

The total length of this presumed pelvis from its base to a point midway between the tips of the two furcations is 10.5 mm. From paired slight processes occurring at the bases of the furcations, there arise two unciform cartilaginous processes, each extending upward in contact with the osseous parts, to a point about 2 mm. from the apex of each furcation. The free ends then deflect inward toward the body of the autosite, the tips being obtusely rounded and in no way connected with the walls of the abdomen.

The confluent femur occurs as a free joint covered with skin, and is attached by muscle, and lateral tendons, to the symphysis pubis, a single caput femoris of minute size occurring directly behind toward the ventral aspect of the autosite. The total length of this bone is 16 mm. At its lower end it broadens out to form three distinct series of condyles articulating with the stunted tibiae. The patellae, as already stated, appear to be absent, and the fibulae, if present, are fused with the tibiae. What may perhaps be termed the outer pair of these bones are of even length, viz. 5 mm., whereas the single centre one is 7 mm.

The two outer tarso-metatarsi are large in proportion to the tibiae, each being 21 mm. in total length and covered with scaly integument. The hind toe in each is lacking. The right foot otherwise is normal in structure, but the left lacks the third toe, its place being taken by a broad elliptical flap of web membrane.

The left tarso-metatarsus and foot, moreover, are directed inward toward the body of the autosite, presenting a three-quarter plantar aspect when the specimen is viewed from the front.

In the central limb, as previously stated, the tarso-metatarsus is represented merely as a spike-like projection 6 mm. in length.

The subject of the present paper is interesting mainly in the fact that the supernumerary paired limbs are again partially dichomotised by the presence, in articulation with the confluent femur, of a third tibia and tarso-metatarsus, the latter imperfectly formed and stunted.

For assistance in the preparation of this paper my thanks are due to Mr. John Hopkinson, F.L.S., F.Z.S., and Mr. E. Leonard Gill, M.Sc.

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May 3, 1910.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President,  
in the Chair.

The Secretary exhibited a photograph of a Giraffe, kindly lent him by Mr. Carl Hagenbeck. The animal was an adult female 3.30 metres in height, obtained in Gallaland, East Africa, and was in the possession of Mr. Hagenbeck. It displayed a reticulate coloration, in which the lighter areas were reduced to narrow lines, clearly on the neck and body, but the hind-quarters were blotched, while the spotting came lower down on the legs than in the typical *Giraffa reticulata*. It possibly represented a type intermediate between *G. reticulata* and *G. camelopardalis*, but it was to be remembered that the specimen was a female, and that females did not exhibit the typical coloration so conspicuously as old males.

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Mr. E. E. Austen, F.Z.S., exhibited a specimen of a rare Fly (*Cephenomyia ulrichii* Brauer) from East Prussia, parasitic in the larval stage in the throat of the Elk (*Alces machlis* Ogilby), and remarked on its habits and those of allied species. This specimen had been recently acquired by the Hon. Charles Rothschild and presented by him to the British Museum.

---

Dr. R. A. O'Brien, introduced by Prof. E. A. Minchin, M.A., F.Z.S., exhibited a series of lantern-slides illustrating the habits of the North Queensland Green Tree-Ant (*Oecophylla smaragdina*?). The Green Tree-Ant is found in the open forest

country or "bush," on the edge of the thick jungle or "scrub," along the sea-coast of Northern Queensland. It is a very active pugnacious insect, from half to three-quarters of an inch long, living wholly or almost wholly in trees. In riding through the country one is frequently covered with the actively-biting insects which fall from a bough touched in passing. Fortunately the bite, though momentarily severe, is not followed by any subsequent irritation.

The nest is built on the bough of a tree and consists of a very large number of leaves, generally fresh and green. These are matted together with a gelatinous material exuded from larvae which the worker ants bring up to the site of the projected nest, where other ants hold the edges of adjacent leaves together. This process is repeated until the bundle may be several feet in diameter.

The bridge formed of the bodies of the ants shown on the screen was re-formed, when broken, by festoons of ants hanging from the upper leaf until some of them, dropping from the festoon, joined momentarily with others on top of the leaf and twigs below. Others quickly joined in strengthening the bridge until it was about four ants' width and eight ants' length. Then the one leaf was seen to be dragged slowly nearer the other, decreasing the bridge to five ants' length, and at this stage it remained for several days, when I left the place.

The ants "on duty" in the bridge over which other ants ran to and fro carrying their "game" were watched carefully for 80 minutes, and none in the centre of the bridge was relieved during that time—a rather remarkable feat of strength and endurance.

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On a new Trypanoplasm, *T. dendroceli*, sp. n., from  
*Dendrocaelum lacteum*.

Dr. H. B. Fantham, F.Z.S., exhibited, on behalf of Miss Annie Porter, D.Sc., and himself, preparations and original drawings of a new *Trypanoplasma* (*Cryptobia*) from the alimentary tract of *Dendrocaelum lacteum*. In some of the preparations the living organisms were shown. The parasites measured from  $20\ \mu$  to  $40\ \mu$  long approximately. They were biflagellate, the posterior flagellum forming a border to the undulating membrane. The blepharoplast (kinetoculus) was large and often somewhat curved. It was proposed to call the parasite *Trypanoplasma* (*Cryptobia*) *dendroceli*. There was evidence of hereditary infection of the Planarian by the *Trypanoplasma*, for the parasites had been seen to enter the eggs of the host, and in some cases to divide longitudinally therein.

Breeding-experiments on *Dendrocaelum* were in progress in order to obtain further information concerning the hereditary transmission of the parasite. Dr. Fantham and Miss Porter thought

it probable that the heredit of the transference of the try method was not the only means seen Trypanoplasms become parasite from host to host. They had probably resting forms when found, the rounded parasites being from the host in this condition, perhaps, encysted and passed out had also been seen to do this. Living flagellate Trypanoplasms Fresh *Dendrocoelum lacteum* pass out of the host on a few occasions. mouth, by ingesting *lacteum* may thus become infected by the with their food. Other flagellate or rounded Trypanoplasms

It is of interest to note that, while the food of *Dendrocoelum* in its natural environment consists of animal matter plant tissues, Annelids, Molluscs, and Crustacea together with bled by us, yet many of the infected Planarians which were vegetative. Dr. Fantham and Miss Porter were kept as compulsory Sojourners throughout their existence.

As far as is known, this is the first record of the occurrence of a Trypanoplasma in the Platyhelminthes.

Hitherto Trypanoplasms had been described from the blood of a number of freshwater fishes, in the alimentary tracts of certain leeches that feed on the fish, and in the intestine of certain marine fishes. The genus *Trypanoplasma* was created in 1902 by Laveran and Mesnil, the type-species being *T. borreli* in the blood of the rudd. *Cryptobia helici* of Leidy (*Bodo helici* of Diesing), from the reproductive organs of snails, was stated by Friedrich (1909) to be a Trypanoplasma. Crawley (1909) claimed that the generic name *Cryptobia* had priority over *Trypanoplasma*. The diagnosis of *Cryptobia* given by Leidy was, however, rather vague.

There was also the interesting and closely allied genus *Trypanophis*, studied by Poche and Keysselitz for flagellates parasitic in the coelenteric cavity of certain Siphonophores. The genus *Trypanophis* was merged in that of *Trypanoplasma* by some authorities, for example, Léger.

Dr. Fantham and Miss Porter also desired to record the occurrence of a Trypanosome-like flagellate which was seen on rare occasions in the guts of *Dendrocoelum lacteum* and *Polycelis nigra*.

---

The following papers were read :—

1. The Morphology and Life-History of *Eimeria* (*Coccidium*) *avium*: a Sporozoön causing a fatal disease among young Grouse. By H. B. FANTHAM, D.Sc. Lond., B.A. Cantab., A.R.C.S., F.Z.S., as Professor of Biology, Christ's College, Cambridge, Assistant to the Quick of the Grouse Disease Inquiry, and Protozoologist to the Grouse Disease Inquiry.

[Received April 5, 1910.]

(Plates LV.-LVIII.\* and Text-figure Plate 65.)

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## I. INTRODUCTION.

The subject of this memoir is a microscopic, protozoal parasite, which infests the lining epithelium of the alimentary canal of grouse. It belongs to the Coccidia, a group of parasitic Protozoa many of which are known to occur in the digestive tracts of both Vertebrates and Invertebrates. These minute organisms reproduce by means of resistant spores, and belong to that class of the Protozoa known as the Sporozoa. The Coccidia are of economic importance, inasmuch as they destroy the mucous membrane of the intestine of the host, thereby setting up enteritis which is accompanied by diarrhœa, and very often has a fatal effect upon the unfortunate animal harbouring the parasites, especially if the host be young.

Such a disease—termed coccidiosis—has long been known in rabbits, and is often fatal. Occasionally coccidiosis occurs in man. The life-history of a Coccidian parasite is complicated. There are two phases in the life-cycle:—(i) a multiplicative phase within the cells of the gut-epithelium of the host, and (ii) a reproductive phase leading, after a sexual act, to the formation of

\* For explanation of the Plates see p. 690.

towards the macrogametes. The microgametes swarm round the micropyle of the macrogamete (Pl. LVII. fig. 47<sup>\*</sup>) and several have been seen trying to enter it simultaneously. The nucleus of the macrogamete travels upwards nearer the micropyle, and before long, one microgamete effects an entry (fig. 47<sup>\*</sup>), appears to bore its way into the female, reach the nucleus and finally be lost to view. The macrogamete secretes a plug of protoplasm across the micropyle, whereby other microgametes are excluded, and the individuals thus shut out degenerate (fig. 48). Such is the process of conjugation as seen in the living organism, and the evidence of stained preparations is fully confirmatory of what has just been described.

Owing to the presence of granules in the macrogamete it is extremely difficult to follow the subsequent stages of fertilisation. Occasionally there are indications of a fertilisation spindle (figs. 50, 51), but the nature of the material frequently precluded observation of the same.

The term "fertilisation spindle" is not exactly a happy one, for the object of that structure is the intimate intermingling of the chromatin of the uniting gametes.

#### (e) *Sporogony.*

After the microgamete has reached the nucleus of the macrogamete, fusion occurs and a zygote is produced. The contents of the zygote at first fill the oval oöcyst (Pl. LVII. figs. 49-52) but gradually they shrink away from the poles†. The oöcyst itself may increase slightly in size during the concentration of its contents, which ultimately form a globular mass, consisting of cytoplasm rich in fatty matters, within which is a nucleus, usually centrally placed.

The nucleus of the zygote proceeds to divide directly first into two (figs. 53, 56) and then into four (fig. 54), the divisions following one another very rapidly. The granular protoplasm segments around the nuclei, and four sporoblasts (fig. 57) are produced, each sporoblast separating from its neighbours as a small, rounded body (figs. 55-57). Occasionally oöcysts containing two ovoid masses of protoplasm (fig. 82) are seen, but as a rule the form containing four sporoblasts is the one found, the four sporoblasts being formed almost concurrently. The sporoblasts become ovoid (Pl. LVII. fig. 58; Pl. LVIII. fig. 68) and each gradually secretes a tough, chitinous sporocyst, usually differentiated as epispore and endospore, and so becomes a firm, resistant spore (Pl. LVIII. figs. 71-76). A minute amount of the cytoplasm of the zygote is not used in spore formation, but remains within the zygote as a small crystal residuum.

The sporocysts continue within the oöcysts for some time,

\* See also Pl. LXII. fig. 3 of my paper on Experimental Coccidiosis (this Journal).

† In some cases the zygote contents of the oöcyst may be slightly nearer one pole than the other.

during which period each sporocyst undergoes developmental changes, leading to the production of actively motile sporozoites. The contents of the spore at first are homogeneous (Pl. LVIII. figs. 68-70), but gradually two refractile bodies or vacuoles appear at either end (fig. 73), and the protoplasm gradually concentrates into two masses, just internal to each vacuole. The nucleus is at first central, but divides into two, and the halves migrate to the opposite poles of the sporocyst (Pl. LVII. fig. 58). The protoplasmic masses gradually displace the polar vesicles, so that the two vacuoles move towards the centre and coalesce (Pl. LVIII. fig. 73), leaving nearly all the protoplasm of the sporocyst in two masses, one at each end (fig. 71). Each of the protoplasmic masses gradually becomes vermiform, extending along one edge of the spore (figs. 71, 72). Two vermiform sporozoites are thus formed (figs. 72, 74), sometimes with their more rounded ends placed at opposite ends of the sporocyst (tête-bêche) (figs. 72, 74, 75), sometimes with the slightly swollen ends side by side (Pl. LVII. fig. 59, Pl. LVIII. fig. 76), the sporozoites being capable of movement within the spore just previous to their escape. There is a slight sporul residuum.

The sporocysts when quite ripe tend to become more pointed at one end (Pl. LVII. fig. 60, Pl. LVIII. figs. 71, 75, 76), where a slight thickening or small Stieda's plate (fig. 71) may appear, which is a point of weakness, for here a rupture may occur under the action of the digestive juices of the fresh host, forming a sort of micropyle through which the sporozoites escape. Partially ruptured sporocysts are sometimes found (Pl. LVII. figs. 59, 60). In the case of grouse chicks dying from acute coccidiosis, ripe sporocysts have been found in the caecal walls themselves, as well as in the caecal contents, though usually mature sporocysts are found in caecal droppings that have been exposed.

The oöcysts of *Eimeria avium* show a fair amount of variation among themselves. Usually the oöcysts are oval (Pl. LVIII. figs. 65-68, 71, 72, 77, 78), actually measured specimens varying from  $25\mu$  to  $35\mu$  in length and from  $14\mu$  to  $20\mu$  in breadth. Sometimes the oöcysts are not oval but subspherical (fig. 70), and these are from  $18\mu$  to  $20\mu$  in diameter. Somewhat pyriform or egg-shaped oöcysts (fig. 69) are intermediate in size between the oval and subspherical forms. Morse (1908) noted the occurrence of both round and oval oöcysts when investigating white diarrhoea of fowls, in which coccidiosis played an important part.

Among the oöcysts of *E. avium* certain were found with somewhat squarish ends (fig. 78) while others had a slight depression at the apex (fig. 79), but their development was identical with that of the more common forms. Occasionally, oöcysts with two sporocysts only (figs. 81, 82) were found, but these were abnormal forms, as was also a parasite (fig. 83) in

which the cytoplasm extended in a cone or funnel-like fashion to the edge of the oöcyst.

The size and shape of the oöcysts are largely a factor of the space in which the macrogamete develops and the amount of food available for the parasite. When there are many *Eimeria* present in any particular region of the gut, the oöcysts produced are relatively small, while where abundance of space and nourishment are available, the oöcysts tend to be large.

From experiments made by feeding birds with Coccidian oöcysts, I conclude that schizogony takes from four to five days. Uninucleate oöcysts mature their sporocysts in two to three days. The period for the total life-history of the parasite would be from eight to ten days.

The larvæ and imagines of *Scatophaga stercoraria*, the dung-fly, ingest the oöcysts of *E. avium* along with the grouse fæces. The oöcysts pass through the bodies of the larvæ uninjured, and are scattered with the excrement, thus serving to disperse the spores to some extent.

## V. SUMMARY OF THE LIFE-HISTORY OF *EIMERIA AVIUM*.

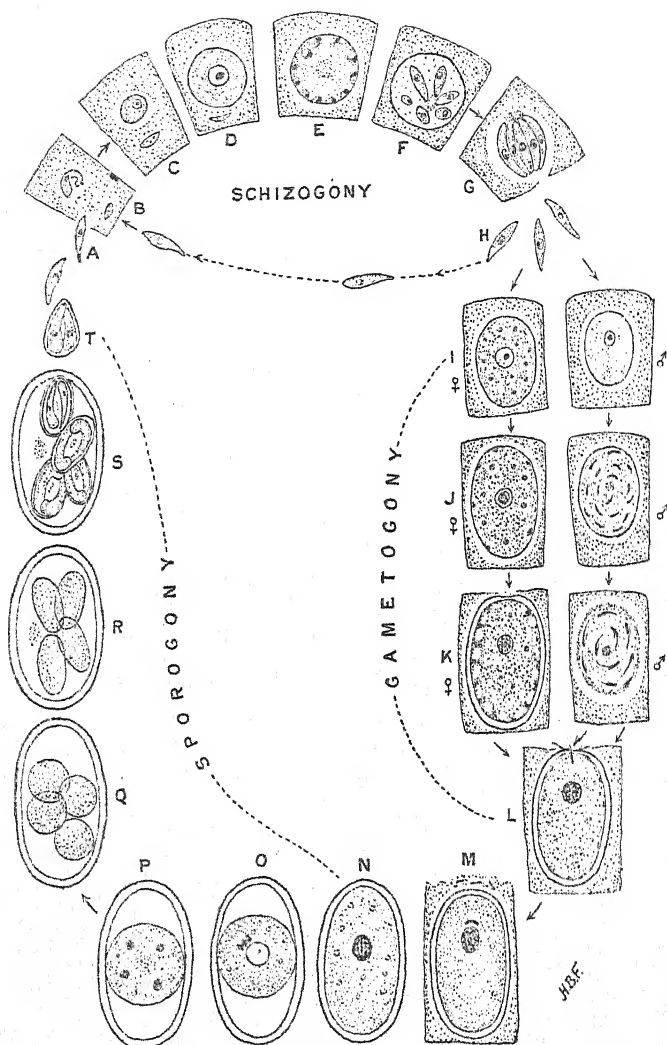
The life cycle of *Eimeria avium* is complicated, even though the organism completes its development within one host. The life-history may be represented diagrammatically as in text-fig. 65, A-T (p. 684). Beginning as a sporozoite (Pl. LV. fig. 2; text-fig. 65, A) liberated by the action of the pancreatic juice of the grouse, the parasite rapidly penetrates an epithelial cell of the duodenum (text-fig. 65, B), and, entering the cell, rounds up (text-fig. 65, C) and becomes a passive growing trophozoite (Pl. LV. figs. 3-7; text-fig. 65, D). After a period of rapid growth, during which time the trophozoite (figs. 8-11) practically destroys the cell harbouring it, the parasite enters upon an asexual, multiplicative phase termed schizogony.

The schizont is at first uninucleate (fig. 12; text-fig. 65, D) but the nucleus soon fragments (figs. 12, 13), the daughter nuclei migrate to the periphery (figs. 14-16; text-fig. 65, E), cytoplasm segregates around each (text-fig. 65, F), and the daughter forms thus produced become meridionally arranged, like the segments of an orange, the arrangement of the merozoites being "en barillet" (Pl. LV. figs. 17-22, Pl. LVI. figs. 23-25; text-fig. 65, G).

Each merozoite is a small, vermicular organism, having a nucleus with a somewhat ill-defined karyosome usually to one side (fig. 24). The groups of merozoites break up (text-fig. 65, H), and the free germs seek out and enter an hitherto uninfected cell where the parasite again assumes the trophic phase and then undergoes division as before. Several successive generations of schizonts and merozoites are thus produced, resulting in a great destruction of the gut epithelium of the host. Finally a limit is



Text-fig. 65.

DIAGRAM of Life-cycle of *Eimeria (Coccidium) avium*.

D-H represent Schizogony. I-L, Gametogony. N-T, Sporogony.

Epithelial host-cells diagrammatically outlined.

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| <p>A. Sporozoite which penetrates epithelial cell of the duodenum of the host.</p> <p>B. Sporozoite curving on itself before becoming rounded within the host cell.</p> <p>C. Young, uninucleate trophozoite.</p> <p>D. Fully grown trophozoite or uninucleate schizont.</p> | <p>E. Schizont with numerous daughter nuclei peripherally arranged, differentiating to form merozoites (seen in transverse section).</p> <p>F. Schizont showing further differentiation of merozoites (seen in oblique section).</p> |
|--|--|

reached to the ability of the host to provide nourishment and to the multiplicative powers of the parasite, and this results in the onset of sexual differentiation. Gametogony may occur both in the duodenum and cæcum.

Certain schizonts become considerably modified in one of two directions. In the first case, food-material accumulates, and a large, uninucleate food-laden form is produced (figs. 26-30). This is the macrogametocyte (text-fig. 65, I ♀), destined to give rise to a single macrogamete (text-fig. 65, J ♀). In the second instance (text-fig. 65, I ♂), nuclear multiplication of a finely granular parasite (Pl. LVII. fig. 37) occurs, and the many minute nuclei produced reach the periphery of the host-cell (figs. 38-42), and ultimately the now multinucleate microgametocyte (text-fig. 65, J ♂) gives rise to a large number of small, motile microgametes (figs. 43-46; text-fig. 65, K ♂). The macrogamete early on invests itself with a cyst-wall (figs. 35, 36) in which a thin part or micropyle is left for the entry of the microgamete (figs. 47, 48; text-fig. 65, K ♀). This oöcyst-wall is formed while the parasite is within the epithelium.

Fertilisation (figs. 47, 48; text-fig. 65, L) occurs—the process

#### Explanation of Text-fig. 65 continued (see opposite).

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|---|--|
| <p>G. Merozoites arranged "en barillet," about to issue from host cell. At one end of the cluster residual protoplasm is seen.</p> <p>H. Free merozoites, each with a small karyosome.</p> <p>I. <br/>         ♀. Young macrogametocyte with chromatoid granules.<br/>         ♂. Young microgametocyte with fine granulations.</p> <p>J. <br/>         ♀. Macrogamete with round nucleus and chromatoid granules distributed through the cytoplasm.<br/>         ♂. Microgametocyte with nucleus divided to form a large number of bent rod-like portions, the future microgametes. Remains of karyosome seen in centre.</p> <p>K. <br/>         ♀. Macrogamete showing plastinoid granules, the chromatoid granules being largely used up in forming the wall with which the macrogamete has invested itself, the remaining chromatoid granules being arranged between the plastinoid granules.<br/>         ♂. Microgametocyte with many biflagellate microgametes about to separate from it. Karyosome left at the centre.</p> <p>L. Fertilisation. One microgamete is penetrating the macrogamete, while other male cells are near the micropyle but will be excluded.</p> | <p>M. Fertilisation. The male pronucleus which entered through a micropyle is lying above the female chromatin. Degenerating microgametes are shown outside the oöcyst.</p> <p>N. Oöcyst (encysted zygote) with protoplasmic contents filling it completely. Nucleus with signs of fertilisation spindle.</p> <p>O. Oöcyst with contents concentrated, forming a central, spherical mass which has a vacuole in the middle and the nucleus to one side. Many such cysts seen in infected caecal droppings.</p> <p>P. Oöcyst with four nuclei.</p> <p>Q. Oöcyst with contents segmented to form four rounded sporoblasts (as seen in fresh preparations).</p> <p>R. Oöcyst with four sporoblasts which have grown oval and are becoming sporocysts; the small cystal residuum seen to one side.</p> <p>S. Oöcyst with four sporocysts in each of which two sporozoites are differentiated. The oöcyst in this condition ultimately opens, liberating the sporocysts, the upper one of which is seen about to issue from the oöcyst. Slight cystal residuum. Sporal residuum in each sporocyst.</p> <p>T. Sporocyst which has issued from oöcyst. Two sporozoites are within it and have assumed the position most suitable for emergence.</p> |
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has been watched in life—and the micropyle is then closed (figs. 49–51; text-fig. 65, M). The fertilised oöcyst (text-fig. 65, N) then passes into the lumen of the gut and is voided with the faeces of the grouse. The further development of the oöcyst largely depends on climatic conditions. Under the influence of warmth and moisture, the contents of the oval oöcyst (Pl. LVII. fig. 52, Pl. LVIII. figs. 61, 62, 64) shrink away from the poles and become a rounded, central mass (figs. 65, 77, 78; text-fig. 65, O). The nucleus rapidly divides into two (Pl. LVII. fig. 56), then four (fig. 54; text-fig. 65, P); each nucleus has protoplasm segregate around it (figs. 55, 67, 70; text-fig. 65, Q), a wall is secreted, and the net result is that four sporocysts (figs. 58, 71–76; text-fig. 65, R) are produced within the oöcyst. Within each sporocyst, two sporozoites gradually differentiate (figs. 58–60, 71–76; text-fig. 65, S), and when the sporocyst (text-fig. 65, T) is ingested by a new host, the sporozoites creep out of the sporocyst softened by the pancreatic juice of the new host and proceed to attack the epithelium of the gut, producing thereby the primary infection of the bird.

The main differences between *Eimeria avium* (Silvestrini and Rivolta) and *E. schubergi* (Schaudinn) may be briefly summarised:—

1. *E. avium* is smaller than *E. schubergi*.
2. The merozoites of *E. avium* are arranged 'en barillet,' those of *E. schubergi* 'en rosace.'
3. Precocious encystment of *E. avium* occurs before fertilisation. This is not the case with *E. schubergi*.
4. Fertilisation in *E. avium* is micropylar; in *E. schubergi* a cone of reception is formed by the macrogamete.
5. The macrogamete of *E. avium* contains much more deeply staining reserve food-material than that of *E. schubergi*, thereby increasing the difficulty of minute examination of the parasite.
6. The cysts of *E. avium* are oval, those of *E. schubergi* are round.

## VI. THE EFFECT OF *EIMERIA AVIUM* ON THE HOST.

The effect of coccidiosis on the grouse may now be considered briefly, fuller details regarding the symptoms of the disease and its effects being given in my paper relating to experimental coccidiosis (P. Z. S. 1910, pp. 708–722).

*External effects.*—The chief external evidence of coccidiosis is the pale colour and great fluidity of the caecal (soft) droppings of the grouse, the pale tint being due to myriads of oöcysts and the condition being that of diarrhoea. Sportsmen and keepers have noted diarrhoea as a symptom of "grouse disease." A similar disease in fowls is known among poultry-men as "white diarrhoea." As the Coccidian parasites cause great denudation

of the intestinal epithelium, digestive derangements are brought about, and consequent on this, malnutrition occurs and the bird becomes very emaciated and "anæmic." Feathering also is poor and ragged, leg weakness is fairly common, and a peculiar bluish tint is sometimes seen at the cere, ears and other parts.

*Distribution and Effects on Internal Organs.*

*Eimeria avium* appears to be purely a parasite of the gut of the grouse and does not affect such gut diverticula as the liver. The crop and gizzard of infected birds are rarely parasitised, though they may contain oöcysts in the condition in which they have been ingested with food. Examination of the duodenum shows that the sporocysts ingested with the food are attacked by the pancreatic juice (as I have proved by pancreatic digestion experiments, using both natural pancreatic juice and trypsin), and the sporozoites are set free. These invade the tissue of the duodenum, rapidly become schizonts and multiply, the result being that the duodenum is often riddled by the parasites, and consequently inflamed. Both the villi and the crypts of Lieberkühn are attacked, and the parasites have also been found, though much more rarely, in the submucosa. Great hypertrophy followed by atrophy of the epithelial host cell occurs, and the tissue attacked is often reduced to a finely granular, structureless mass. Desquamation of the gut is common, and epithelium containing various developmental stages of the parasite can be found floating free in the gut contents.

Some of the merozoites formed in the duodenum pass down the gut, reach the cæca and re-commence their life cycle there. Active schizogony and sporogony go on in the cæca\*, chiefly in the epithelium, very rarely in the submucosa. Often the cæca are as heavily parasitised as the duodenum, whole areas being completely denuded of the epithelium, especially when the fertilised oöcysts pass outwards into the cæcal contents. The walls of the cæca are often rendered very thin and tender by the action, direct and indirect, of the parasite. Ripe oöcysts and sporocysts occur in the lumen of the cæca of dying chicks.

Podwyszołski (1890) stated that he found Coccidian oöcysts in the vitellus of eggs of fowls, especially in summer. He considered it possible that the cysts were derived from Coccidia in the oviduct of the mother, or perhaps from intestinal Coccidia which had ascended by way of the cloaca. I think that cloacal contamination was the more probable, for I have never seen Coccidia in the genitalia of adult grouse examined.

A reflex of coccidiosis is seen in the blood of infected birds, where polymorphonuclear leucocytosis is induced.

\* Coccidiosis may sometimes occur along the entire length of the small intestine, and gametes may be formed far forward, in the duodenum.

Lesions caused by coccidia in the mucous membrane may admit bacteria to the circulation of the host. [Cobbett and Graham-Smith (1910), pp. 24, 25]. Rettger (1909) believes that "white diarrhoea" of fowls in America is due to a bacterium, while Morse (1908) considers that it is primarily due to coccidiosis. The discrepancy between the results of these American workers is thus capable of explanation.

## VII. CONCLUDING REMARKS.

*Eimeria avium* of grouse is not restricted to this particular bird, for by administering faeces containing oöcysts from diseased grouse to young fowl chicks and pigeons, I have been able to reproduce the disease exactly as it occurs in grouse (p. 674). McFadyean (1894) found coccidiosis in pheasants, while "white diarrhoea" of fowls has been the subject of much investigation, particularly recently in America, where Morse (1908) and Hadley (1909) have worked on the subject. Morse's account of preventive measures is very good and he also notes coccidiosis in many other birds, but the figures of the complete life-cycle of the parasite are not yet published. Labbé (1896) also has described coccidiosis in certain marine birds.

Though coccidiosis is peculiarly fatal to grouse chicks during the first few weeks of their lives, adult grouse also can become infected, for I have examined an adult bird that probably died of coccidiosis. Old birds in the chronic condition serve as reservoirs of oöcysts and so may form sources of new infections on the moors. All infected corpses should be burned, *not* buried.

I may add that, while correcting the proofs of this memoir, I have been able to examine pheasant chicks dying from coccidiosis, the birds being obtained through the courtesy of Drs. Shipley and Hammond-Smith from various parts of England during June and July 1910.

The economic importance of coccidiosis in birds, especially in the young, is evident, and I trust that this work, which to the best of my belief is the first fully illustrated and detailed life-history of an avian *Coccidium*, may draw more attention to a subject both of great scientific interest and of practical importance.

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## EXPLANATION OF PLATES LV.-LVIII.

All figures outlined with Abbé-Zeiss camera lucida, from stained preparations (sections of infected gut) except where otherwise stated. Zeiss 2 mm. apochromatic immersion objective and compensating ocular 8 usually employed. The magnification is about 1400 diameters, except where indicated otherwise. Many parasites are represented lying in portions of the degenerating epithelium surrounding them.

## PLATE LV.

Fig. 1. Portion of gut (cæcum) of infected grouse to show mucous membrane riddled with parasites. Many stages in life-history of *Eimeria avium* shown therein.

2. Sporozoite from duodenum, showing its trail stained.
3. Sporozoite penetrating epithelium.
4. Young parasite just entered epithelium, by fine channel which is still open. The entering parasite is by the side of a slightly older (rounded) parasite or young trophozoite.
- 5, 6. Parasites beginning to become round.
7. Sporozoite, curved on itself, preparatory to becoming round. Duodenum.
8. Round, young parasite, with relatively vesicular nucleus containing karyosome.
9. Young trophozoite, as yet oval in shape, lying in relatively large space in the gut-wall.
- 10, 11. Round trophozoites, with large nuclei each containing a karyosome. Large space surrounding parasite shown in fig. 11.
12. (a) Uninucleate, full-grown trophozoite, becoming a schizont.  
(b) Schizont in which nucleus is dividing. Duodenum.
13. Schizont in process of nuclear fragmentation.
- 14, 15, 16, 17. Schizonts containing many nuclei which go to the periphery of the cell. Very small karyosome differentiating to one side in each daughter nucleus.
- 18, 19. Developing merozoites.
- 20-22. Merozoites arranging themselves "en barillet," with residual protoplasm in middle or to one end.

Several smaller and younger parasites shown by the side of the "barillet" in fig. 22.

## PLATE LVI.

Fig. 23, 24. Groups of merozoites, beginning to separate.

Fig. 23 magnification 1400. Fig. 24 magnification 1600.

25. Small schizont, containing five young merozoites—seen in cross-section. Cæcum.
26. Macrogametocyte, with granules of reserve food-material.
- 27, 28. Young macrogametocytes.
29. Longitudinal section of macrogamete, stained with Delafield's hæmatoxylin, showing deeply staining chromatoid granules, a few of which are surrounded by clearer areas of plastin.
30. Transverse section of older macrogamete, stained with iron hæmatoxylin and picro-fuchsin, with cyst just formed. Plastinoid granules well defined; chromatoid granules (largely used in cyst formation) small and in between the plastinoid granules.
- 31, 32. Macrogametes, in section, as stained by Delafield's hæmatoxylin. Chromatoid and plastinoid granules alternating. Plastinoid granules do not stain with hæmatoxylin.  $\times 1600$ .  
Young macrogametocytes seen in the vicinity.
- 33, 34. Macrogametes with chromatoid and plastinoid granules, after careful staining with iron hæmatoxylin and picro-fuchsin. In fig. 34 chromatoid granules are seen passing to the periphery, to form the inner wall of the mature macrogamete.
- 35, 36. Mature macrogametes. Remains of chromatoid granules seen attached to inner wall of cyst.

## PLATE LVII.

Fig. 37. Microgametocyte or male mother cell.

38-40. Nuclear fragmentation of microgametocyte. In fig. 38 remains of parent karyosome seen. In fig. 40 young microgametes arranged along meridians.

41, 42. Young microgametes at periphery of mother cell.

43-45. Separation of the clusters of microgametes.

46. Free microgametes.

47. Fertilisation. One microgamete has gained access to the female pronucleus. The micropyle has closed, and the microgametes left outside will degenerate.

48. Fertilised oöcyst. Zygote nucleus beginning to form a fertilisation spindle. Remains of microgametes on outside of cyst.

49. Zygote in oöcyst just after fertilisation.

50, 51. Show "fertilisation spindle"—not very clearly differentiated in *Eimeria avium*.

52, 53. Longitudinal and transverse sections of oöcysts, containing rather a large amount of reserve material—as judged by staining (hæmatoxylin). In fig. 53 the zygote nucleus shows signs of dividing.

54. Oöcyst with four nuclei, one ready for each sporoblast. Safranin, Lichtgrün.

55. Small oöcyst with four round sporoblasts. Paracarmin.

56. Oöcyst, showing segmentation into four sporoblasts. From lumen of cæcum of dying grouse chick.

57. Oöcyst, with four ovoid sporocysts, and cystal residuum, containing minute dot of chromatin (? remains of karyosome of macrogamete). Cut obliquely.

58. Oöcysts with four sporocysts showing commencement of differentiation (polar separation of nuclei) into sporozoites. Paracarmin.

59, 60. Sporocysts, each with two sporozoites. Dehiscence represented in fig. 60.

## PLATE LVIII.

Mostly from fresh preparations.  $\times 1000$ .

Fig. 61. Zygote nearly filling oöcyst. Culture of caecal contents of grouse containing such oöcysts made and examined for four days subsequently.

62, 63, 64, 66. Development at beginning of second day.

65. Cyst uninucleate, such as is frequently seen in fresh faeces.

67. Oöcyst with four sporoblasts, as seen at end of second day, and on third day.

68. Oöcyst with four ovoid sporoblasts, as seen in cultures on the third day.

69-70. Illustrate three common forms of oöcyst of *E. avium*—oval, egg-shaped, and rounded. There is variation among the oöcysts.

71. Oöcyst with four sporocysts, in each of which sporozoites are differentiating.

72. Oöcyst with four sporocysts, nearly ripe, each containing two sporozoites. From partially dried caecal droppings, taken from grouse moor.

73. Ripe oöcyst dehiscing—one sporocyst outside, with sporozoite nuclei at poles, and central vacuole. Sporocyst inside oöcyst shows polar vacuoles.

74. Free sporocyst, from faeces. Sporocyst contains two sporozoites, arranged "tête bêche," and sporal residuum.

75, 76. Sporocysts, each with two sporozoites.

77. Oöcyst, commonly occurring in fresh droppings.

78. Oöcyst with somewhat square ends.

79. Oöcyst with depression (thin place in cyst-wall) at one end.

80. Zygote in oöcyst—zygote nucleus dividing into two. Stained preparation.

81. Oöcyst containing two precociously separated sporoblasts. There should be, normally, four sporoblasts. Probably the oöcyst represented will degenerate. Stained preparation.

82. Oöcyst with two sporoblasts. Very few of these seen. Possibly abnormal. The four sporoblasts should be formed almost concurrently in the normal cyst.

83. Oöcyst showing protoplasmic contents in form of cone-like projection attached at one point to the cyst. Development retarded, after keeping three weeks in water.



2. Observations on the Parasitic Protozoa of the Red Grouse (*Lagopus scoticus*), with a Note on the Grouse Fly. By H. B. FANTHAM, D.Sc. Lond., B.A. Cantab., A.R.C.S., F.Z.S., Christ's College, Cambridge, Assistant to the Quick Professor of Biology, Cambridge, and Protozoologist to the Grouse Disease Inquiry.

[Received April 5, 1910.]

(Plates LIX.-LXI.\*)

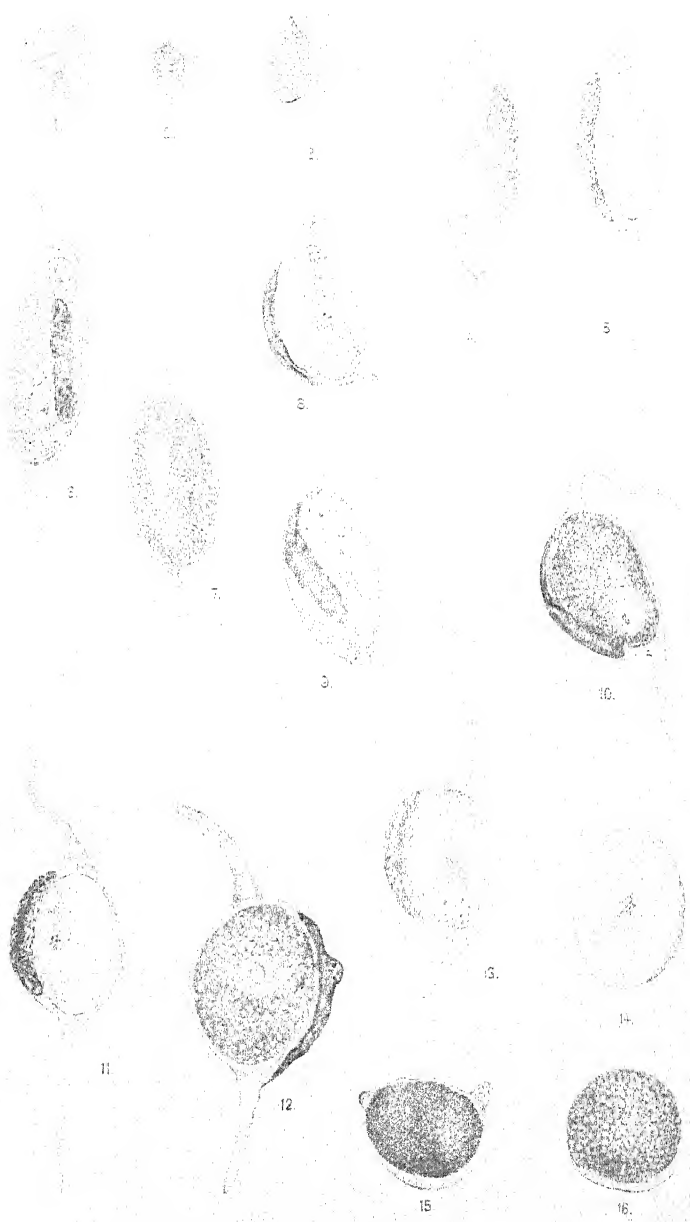
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# INTRODUCTION.

In the following paper are recorded observations made on the various parasitic Protozoa found in Grouse examined in connection with the Grouse Disease Inquiry. The observations were, by force of circumstances, limited to one season, and so the accounts of some of the parasites are consequently incomplete. The parasitic Protozoön of greatest economic importance, and to which most attention had to be devoted, is *Eimeria (Coccidium) avium*, which is the pathogenic agent of a fatal disease in grouse-chicks, particularly prevalent in the spring and early summer. The morphology and life-history of *Eimeria avium*, and the results of experimental studies on avian coccidiosis are set

\* For explanation of the Plates see p. 707.

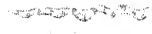


3-4 Fencham, Tex.

2 Wilson, Cambridge.

LEUCOCYTOZOON LOVATI





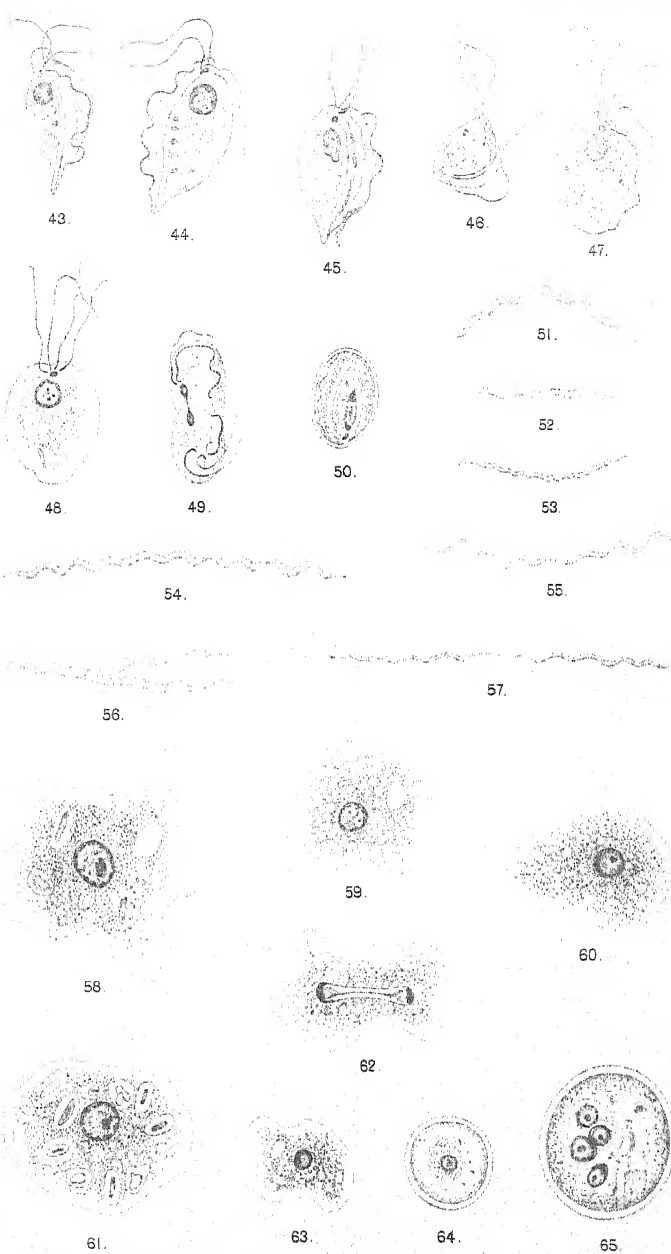
17-21. *Leptocystis* (n. sp.)

22-29. *Spirochaeta* (n. sp.)

30-40. *Spirochaeta* (n. sp.)

41-42. *Haemaphysalis* (n. sp.)





H. A. Parham del.

E. Wilson, Cambridge.

43-50 TRICHOMONAS EBERTHI. 51-57 SPIROCHAETA LOVATI.  
58-65 AMOEBA LAGOPODIS.



forth by me in two other memoirs\*. The remaining Protozoa found in grouse may be conveniently divided into ( $\alpha$ ) parasites of the blood of the bird, ( $\beta$ ) parasites of the alimentary tract of the grouse. So far I have found seven Protozoa parasitic in grouse, exclusive of the *Coccidium* already mentioned.

#### (A) PARASITES FOUND IN THE BLOOD OF GROUSE.

##### Sporozoa—Hæmosporidia.

##### 1. *LEUCOCYTOZOON LOVATI* Seligmann & Sambon, 1907.

(Plates LIX., LX. figs. 1-28.)

##### (a) *Introductory.*

This parasite was discovered in 1907 by Seligmann and Sambon in blood-films of grouse. It was found in one bird not suffering from "grouse-disease." Sambon (1908-9) refers again to the parasite, and states that he found it in five more grouse. Sambon gives five drawings of the parasite.

Personally, I found this parasite in 1909 in three grouse, all of which were in splendid condition, though in one case the spleen was found to be slightly enlarged. The parasites were in no case numerous, and in one bird only the younger stages of the parasite were seen. However, in the two remaining birds I had the good fortune to find the parasites alive in peripheral blood and in heart-blood taken from birds freshly killed. Observations were made on the living parasites, both unstained and after colouring them *intra vitam* with methylene blue (Pl. LX. figs. 17-22). The parasites were also seen while making blood-counts of the avian hosts, when the *Leucocytozoon* stained *intra vitam* with the methyl-violet of Toison's fluid.

##### (b) *The Relation of the Parasite to its Host Cell.*

The nature of the host-cell is controversial, some authorities considering that it is an erythroblast, others that it is a leucocyte, while the views of some of the observers have changed during the course of their investigations. The host-cell clearly does not contain hæmoglobin, and no melanin pigment is excreted by the parasite. The host-cell is at first round or ovoid, containing a rather broad and well-marked nucleus, and so the host-cell must be either a mononuclear leucocyte or an erythroblast. Possibly both these types of cells may be infected. The nature of the host-cell is inherently difficult to determine in view of the fact that all the blood-cells of birds are nucleated. Judging by the size of the nucleus of the host-cell (Pl. LIX. figs. 1-3), I incline to the view that it is a small mononuclear leucocyte or potentially such. Other workers have acknowledged the resemblance of the host-cell to a mononuclear leucocyte. However, the matter can only be definitely settled by researches on the origin and

\* P. Z. S. 1910, pp. 672-691 and 708-722.



either the parasite undergoes a multiplicative stage in some internal organ (though it is stated that the internal organs of the fowls were examined), or a latent phase without increase in numbers of the parasite occurs; or else a re-infection of the host takes place. I have found schizogony of *L. lovati* (see next section) in the spleen of the host, but so far neither time nor material have been available for my observing any possible periodicity in the gametocytes of *L. lovati*, though such may occur.

Gametocytes were found to be rare in the peripheral blood, more numerous in heart-blood, and were also seen in smears of the liver and spleen of infected grouse.

#### (d) *Schizogony.*

Schizogony in the avian Leucocytozoa has not been recorded before. However, in my investigations of *L. lovati*, I have succeeded in finding schizonts of this Leucocytozoön in the spleen of two infected birds (Pl. LX. figs. 23-28). I saw living Leucocytozoa in the heart-blood of these birds, and immediately made fresh smears of the internal organs. In the spleen were found rounded or ovoid bodies—the schizonts—with thin walls, coloured red with Giemsa's stain. These schizonts contained many merozoites (figs. 25, 26). The capsules of the schizonts are probably formed, at least in part, by the remains of the host-cell (fig. 26). The protoplasm of the schizont appeared to be slightly granular (fig. 26). Some of the schizonts already contained a few nuclei in process of multiplication by amitotic binary fissions (figs. 23, 24), while other schizonts contained small vermicular merozoites (figs. 25, 26) which ultimately escape from the mother cell (fig. 26) and may be found free in spleen smears (figs. 27, 28), when their mode of origin and general appearance are clearly grasped. A small amount of residual protoplasm is left behind in the thin membranous remains of the schizont which has just shed its merozoites. The schizonts are from  $11\ \mu$  to  $14\ \mu$  by  $8\ \mu$  to  $11\ \mu$ , and the merozoites are about  $7\ \mu$  in length.

The birds whose spleens contained schizonts of *L. lovati* were not infected with any other Hæmoprotazoön.

Preparations made from the bone-marrow of infected birds, in which schizogony might also take place, did not exhibit developmental forms.

#### (e) *Concluding Remarks.*

The method whereby *Leucocytozoön lovati* is transferred from grouse to grouse has not yet been shown with certainty. The vector or second host of *L. lovati* will probably be found in some blood-sucking insect, which ingests the parasites from one grouse and transfers them to the next bird from which it obtains blood; or perhaps there is a cycle of development of the parasite inside the Arthropod vector.

The grouse-fly (*Ornithomyia lagopodis*) suggests itself as a

likely carrier or second host of *Leucocytozoon lorati*. During my investigations I have dissected several hundreds of grouse-flies. In the gut contents of a very few of these flies I found unicellular motile vermicules, which may have been stages in the life-cycle of *L. lorati* or perhaps of *Hæmoproteus mansonii*. In the grouse-flies dissected I never found cysts, such as occur in the stomachs of mosquitoes which have fed previously on blood infected with malarial parasites.

As before-mentioned (p. 693) *Leucocytozoon lorati*, as it has been found to occur in grouse on the moors, does not appear to be a serious agent of disease.

*HÆMOPROTEUS MANSONI* Sambon, 1908.

(Plate LX. figs. 41-42.)

This parasite of the red blood corpuscles of grouse was recorded by Sambon in 1908, though I am not aware that he has yet published a description or figures\* of the parasite.

In blood-films sent to me from Scotland and taken from two grouse, I found, after staining, a few parasites inside the red blood corpuscles. Two examples of the organism are drawn in Pl. LX. figs. 41, 42. They appear to be young forms of the parasite, one of which showed clearly granules of melanin pigment. I regret that, owing to lack of material, I cannot give a fuller description of the organism.

It is likely that this hæmosporidian is spread from grouse to grouse by the grouse-fly, *Ornithomyia lagopodis*, in the gut of which grouse-blood is found. In the gut-contents of the fly unicellular vermicules, apparently protozoal organisms, were sometimes seen. Further, Sambon states that "in the stomach of one [grouse-] fly, I discovered a few hæmozoin-bearing protozoa, which were no doubt the ookinetes of the *Hæmoproteus mansonii* previously found in the blood of a grouse from Scotland" (Sambon (1909), p. 37).

**Spirochætacea (Proflagellata).**

*SPIROCHÆTA LAGOPODIS*, sp. n.

(Plate LX. figs. 29-40.)

When examining the blood of grouse for parasites, I have occasionally found a few small Spirochætes exhibiting considerable morphological variation (Pl. LX. figs. 29-40). As a Spirochæte has not been previously recorded from the blood of grouse, I have named it *Spirochæta lagopodis*. The Spirochætes were present in

\* Since writing the above I find that figures of *Hæmoproteus mansonii*—which I am informed are from originals supplied by Dr. Sambon—have been published recently in Castellani and Chalmers' "Manual of Tropical Medicine," fig. 55, p. 235.

blood from the heart, liver and spleen of three birds, but were somewhat rare in each case. On one occasion I saw the parasites in life; the remaining preparations were fixed and coloured with Giemsa's stain.

Dr. Sambon (1909) has noted the presence of an unnamed Spirochæte "in smears from the pulp of young feathers, and not in the general circulation" of grouse. It is possible that *Spirochæta lagopodis* and the parasite of feather-pulp may be identical, but as details of the latter parasite are lacking, I cannot establish the identity or otherwise. Dr. Sambon also thinks that lice might act as "alternative hosts" for the Spirochætes. I will return to the subject of transmission later.

*S. lagopodis* is from  $10\mu$  to  $18\mu$  long and is relatively broad for this class of organism. In life it moves actively in the blood of the host, spirally boring its way between the corpuscles. *S. lagopodis* also often entwines one part of its body about the other (fig. 31). The organism usually has tapering ends (figs. 29-40).

Though the Spirochæte is small, stained specimens show a fair amount of structural detail. A narrow undulating membrane (figs. 29-36) is present, and passes spirally round the body. The thickened border of the membrane stains bright red with Giemsa's stain (figs. 29-34), and even when the membrane is closely contracted round the body of the Spirochæte, the border can be distinguished as a bright line (figs. 30, 32).

The chromatin of the Spirochæte is distributed in the form of bars throughout the body (figs. 29-35), and at times these chromatin bars become joined and form a helicoid core (fig. 36) traversing the entire length of the body. This latter condition is comparatively rare. A basal granule is present at either end, and near these granules the membrane is attached. Longitudinal division is usually initiated by fission of the basal granules.

Multiplication of *S. lagopodis* takes place by both longitudinal and transverse division. In longitudinal division rather thick Spirochætes divide (fig. 40), the split extending gradually from one end and the daughter forms diverging more and more until final separation occurs. Transverse division takes place in relatively long organisms (fig. 35) and two daughter forms are produced. The parent organism elongates somewhat during the division. Very minute forms (fig. 39) about  $4\mu$  long are the product of repeated divisions in both directions. Small forms have been seen in the spleen (figs. 38, 39). By reference to growth following division, all the variations in size and form exhibited by *S. lagopodis* may be explained.

Regarding the mode of transmission of *S. lagopodis*, it seems to me that the nymphs of *Ixodes ricinus*, that sometimes infest grouse, may be the carriers of the Spirochætes, for in the gut of nymphs of *Ixodes ricinus* taken from grouse, I have found Spirochætes which may be *S. lagopodis*. During my investigations, I have dissected many Mallophaga, both *Nirmus cameratus* and *Goniodes*

*tetraonis*, but have not found Spirochaetes, though the sperm of these lice are deceptively like Spirochaetes at first sight. Dr. Sambon has suggested that lice act as transmitters of the Spirochete that he found in feather-pulp. This is possible, and as a matter of fact, evidence is accumulating and tending to show that the carrying of disease in a particular host is not restricted to any one species of Arthropod, but that several organisms differing in genera as well as in species, may become active agents in the dissemination of protozoal parasites.

Among Spirochaetes known from the blood of various birds may be mentioned *Spirochaeta gallinarum* of fowls, *S. anserina* of geese, and a Spirochete cultivated by Töpfer from the blood of the owl.

*S. gallinarum* is the pathogenic agent of a fatal disease in fowls, and is spread from bird to bird by the tick, *Argas persicus*.

*S. lagopodis* is much too rare, I think, to be a serious cause of disease in grouse, although leucocytosis was found in a grouse infected with *S. lagopodis*, in the blood of which bird many vacuolated mononuclear leucocytes occurred.

## (B) PARASITES FOUND IN THE ALIMENTARY TRACT OF GROUSE.

### (a) Flagellata.

#### *TRICHOMONAS EBERTHI.*

(Plate LXI. figs. 43-50.)

While examining, on the moors, the caecal contents of grouse—more especially for Spirochaetes—I have sometimes observed a Flagellate Protozoön moving therein.

The parasite was seen to possess an undulating membrane, the vibrations of which often regulated the parasite's active movements; at other times flagella were seen anteriorly whose active forward movements dragged the body of the organism onwards.

The structure of the parasite is complex. The organism closely resembles, both in size and shape, the parasite described recently (1909) by Martin and Robertson from the caeca of the fowl. The flagellate of the fowl, first seen by Eberth in 1862, was named *Trypanosoma eberthi* by Kent (1881), *Spirochaeta eberthi* by Lühe (1906), while Stein, Leuckart, and Laveran and Mesnil more correctly considered it to be a *Trichomonas*. The nomenclature of the parasite is discussed at length by Martin and Robertson (1909). These authors describe both *Trichomonas* and *Monocercomonas* forms as well as a *Trypanosoma*, and state that they "have observed some cases of which the most natural explanation would be to regard the A [*Trypanosoma*], B [*Trichomonas*], and C [*Monocercomonas*] conditions as stages in one life cycle"; otherwise the parasites are distinct and there is a mixed infection.

It seems to me that the flagellate which I have seen in the

cæcum of grouse is best named *Trichomonas eberthi*, though Eberth's original figures published in 1862 do not especially suggest a typical *Trichomonas*. However, the somewhat peculiar shapes figured by Eberth are perhaps due to the fact that the organism is very easily deformed.

In grouse both typical *Trichomonas* (Pl. LXI. figs. 43-46) and *Monocercomonas* (fig. 48) forms were seen in life as well as in fixed and stained preparations (fixed wet with osmic acid and stained with Delafield's hæmatoxylin or Giemsa's stain). The bodies of the parasites vary from  $8\mu$  to  $13\mu$  by  $6\mu$  to  $9\mu$ .

*Trichomonas eberthi* possesses three flagella disposed around a slight cytostomic depression (figs. 43-45), and arising inside the body close to a chromatin granule, the blepharoplast or kinetonucleus. The flagella are often much entangled. There is an undulating membrane with a flagellar border and short free flagellum; the membrane possesses also a chromatic base line on the body as seen in some specimens (fig. 45). There is also a skeletal organella arising at or close to the blepharoplast and running backwards to the posterior (non-flagellar) end of the body, where it may project a little (figs. 43-45). This stiff skeletal rod—which stains blue with Giemsa's stain—is the axostyle. A row of granules or blocks may be seen alongside the axostyle and base line of the membrane—better marked in some specimens than others (figs. 43-45). The nucleus is situated rather nearer the flagellar end of the body close beneath the blepharoplast, and is fairly large and more or less spherical. Chromatin granules are seen within it during the resting state, and a nuclear membrane is present (figs. 43-46).

*Trichomonas eberthi* divides longitudinally. Although I have carefully searched for dividing forms, I have only seen them on two occasions, and then in stained preparations. One of the dividing forms is shown in fig. 49, but I had not sufficient material to follow the details of division. The process of division is well described by Dobell (1909) for *Trichomonas batrachorum*, and by Wenyon (1907) for *T. intestinalis* in the mouse.

Encystment\* of *T. eberthi* occurs (fig. 50). The organism gradually becomes oval in outline, and its body substance concentrates after gradual absorption of the flagella, undulating membrane and axostyle (fig. 50). A thin gelatinous cyst is seen in the specimen drawn (fig. 50). Round, contracted, unencysted forms were also seen; these are probably resting forms.

Aflagellate, irregular, non-motile forms with nucleus and axostyle are occasionally seen. Amœboid forms are, I believe, the result of degeneration.

Sometimes, in stained smears of the cæcal contents of grouse containing *Trichomonas*, I have seen curious ovoid or figure-of-8 bodies which suggest much deformed specimens of *Trichomonas* in which the axostyle acts as a rod around which the flagellar border

\* B. Parisi has recently noted encystment in Trichomonads (Arch. f. Protistenkunde, xix. p. 232).

and strands of the membrane are disposed. Some of these bodies are not unlike Eberth's original figures (1862).

*Monocercomonas* is an ovoid organism possessing four flagella at the broad anterior end of the body (fig. 48) together with a nucleus and blepharoplast. Sometimes one of the flagella trails backward (fig. 47). On one occasion a *Monocercomonas* form with a suggestion of a rudimentary membrane, axostyle and granules was seen (fig. 47). If such a parasite be normal and not deformed, then it would be an intermediate form between *Trichomonas* and *Monocercomonas* (cf. Martin and Robertson's fig. 8).

### (b) Spirochætacea (Proflagellata).

*SPIROCHÆTA LOVATI*, sp. n.

(Plate LXI. figs. 51-57.)

When fresh cæcal contents of certain grouse of various ages were examined microscopically, small active organisms have been seen, moving among the food débris and flora found in the gut. These organisms are Spirochætes, and their presence in the cæcal contents of grouse has also been noticed by Dr. Cobbett in adult grouse, and by Dr. Leiper in a young grouse chick. I have sometimes observed the Spirochætes in the hinder part of the intestine as well as in the cæca.

Having had the opportunity of observing this Spirochæte, which I have named *Spirochæta lovati*, I append a few details regarding its life-history and structure. I may say that the parasite does not appear to have a very deleterious effect on its host.

The organism, as observed in life, occurs in cæcal contents, where it is mingled with semi-fluid food materials, and is often in company with many minute, rod-like bacteria, both free and in colonies, and also small hyphal threads, evidently of some fungus. Because of its associations, the Spirochæte is by no means easy of observation, and much dilution of the cæcal contents to facilitate observation only hastens the death of the Spirochæte. Further, in fixed and stained preparations the Spirochæte itself takes up the stain somewhat faintly.

The movements of the Spirochæte are active and resemble those of the Spirochætes of Lamellibranchs (oysters, fresh-water mussels, *Tapes*) which I have already described (1907, 1908, 1909). "The motion appears to be resolvable into at least two components: (i) An undulatory flexion of the body, mainly for progression, and (ii) a spiral or corkscrew movement of the body as a whole, due to the winding of the membrane." *S. lovati* has a small, but distinct undulating membrane best seen in stained preparations (Pl. LXI. figs. 51-57). The ends of the organism are pointed, the length of the body being from  $16.5\mu$  to  $32.5\mu$ .

In some very narrow forms the relatively long body may be thrown into many waves (fig. 53), but usually four to seven waves

occur along the body (figs. 51, 52, 55). The membrane with its chromatic border is often closely contracted against the body (figs. 53, 55). The chromatin of the Spirochaete is usually present in the form of a number of bars (figs. 51-57) which are probably disposed on a helix as is typical for Spirochaetes.

After examining many specimens of the parasite it was seen that *S. loati* exhibits morphological variation. Thus, the ends of the body usually taper (figs. 58-57), but occasionally are somewhat rounded (figs. 51, 52). Also, the Spirochaetes are of different lengths and breadths, the results of growth and division.

Multiplication of *S. loati* by both longitudinal and transverse division has been seen in life. Division resembles that of *S. recurrentis* and *S. duttoni*, where a periodicity in the direction of division occurs (Fantham and Porter, 1909). Broad Spirochaetes (fig. 51) have been seen to divide longitudinally (fig. 56). Longer Spirochaetes (fig. 54) often divide transversely (fig. 57), elongating somewhat as they do so.

The modes of multiplication and the processes of growth are of the utmost importance in elucidating the morphological variation of Spirochaetes.

### (c) Rhizopoda.

*AMOEBA (ENTAMOEBA) LAGOPODIS*, sp. n.

(Plate LXI, figs. 58-65.)

Living Amoebae were seen by Dr. Shipley (1908-9) in fresh faeces of grouse. I have, on a few occasions, observed Amoebae in the recently voided faeces and in the rectum and intestine of grouse. The living organism was examined both with and without staining *intra vitam*, and a few stained preparations were made with Delafield's hematoxylin after fixation with corrosive-acetic-alcohol or osmic vapour, but the whole of the material was very scanty.

In structure the Amoeba exhibits ectoplasm and endoplasm fairly well differentiated (Pl. LXI, figs. 58-63). The Amoeba moved slowly by sending out pseudopodia in the manner usual to these organisms, the pseudopodia being first chiefly composed of ectoplasm. Very few pseudopodia were sent out at any one time. There is a nearly central nucleus, often possessing a karyosome. Food vacuoles containing partially digested food particles and bacteria were seen (fig. 61). The granular endoplasm may contain a vacuole (figs. 58, 59).

Amoeboid organisms, from the irregularity of their shape, are not easy to measure precisely. More or less rounded forms may measure  $60\mu$  in diameter (fig. 61) with a nucleus  $10\mu$  in diameter. Other specimens of the parasite (figs. 59, 60, 63) measure from  $20\mu$  to  $40\mu$  across, with a nucleus of  $5\mu$  to  $8\mu$  in diameter.

In preparations stained with Delafield's hematoxylin the nucleus was seen to be spherical (figs. 58-61) with a nuclear membrane on which the chromatin could sometimes be clearly

seen in the form of granules (fig. 58). The whole nucleus, however, is somewhat poor in chromatin, though a karyosome may be present (figs. 58, 60, 63) as before-mentioned.

Division by binary fission was seen once in life, the process taking about thirty minutes for completion. The Amœba when first noticed was already elongate and the dividing nucleus appeared as a refractile streak across the body of the parasite. A similar dividing form (fig. 62) was once seen in a fixed and stained preparation. The nucleus was drawn out in the form of a long spindle with a central fibre, which opens out at its extremities into cone-like expansions, perhaps composed of the remains of the fibres of the nuclear spindle. The actual ends of the dividing nucleus were composed of chromatin masses or plates (fig. 62). The division of the cytoplasm was delayed somewhat after that of the nucleus.

Encystment was rarely seen in life, and the full details could not be followed. It was noticed sometimes that, following division, the daughter individuals proceeded to encyst after a short interval and so formed small cysts. In fixed preparations somewhat small uninucleate cysts, about  $12\ \mu$  to  $14\ \mu$  in diameter, were seen (fig. 64). Larger cysts containing four nuclei were also found (fig. 65), but the cysts were not numerous. The larger cysts measured about  $20\ \mu$  in diameter.

I am sorry that opportunity did not arise for me to make an extended study of this parasite.

Although *Entamœba histolytica* (Schaudinn) is the pathogenic agent of a form of dysentery in man, it is not very likely that *Amœba* (*Entamœba*) *lagopodis* is the cause of such a serious disease in grouse, but *A. lagopodis* is more like *Entamœba coli*, which is usually considered to be a well-nigh harmless parasite in the human intestine.

*Amœba meleagridis* (Theobald Smith, 1895), which has been associated with the disease known as "blackhead" in turkeys, is now generally considered to be a stage in the life-history of a *Coccidium*.

#### (d) Sporozoa—Gregarinida.

##### *MONOCYSTIS* sp.

Spores of a Gregarine, almost certainly a species of *Monocystis*, were occasionally found in the contents of the gut of a few grouse from the Lowlands of Scotland and the North of England. The spores present much the same features as those commonly occurring in the Earthworm, and show the same pseudo-navicellar appearance. The spores seem to pass through the alimentary canal of the grouse intact. The grouse acquire the spores accidentally by way of their food (though earthworms are not common on many grouse moors), and the spores have no ill effect on the birds. Probably the internal heat of the bird's body aids in the development of the sporozoites within the sporocysts,



though the spores are not acted on externally by the digestive juices of the host.

Uninjured spores of Gregarines have been observed by L. Pfeiffer in the alimentary tract and fæces of various birds.

## APPENDIX.

### NOTE ON THE GROUSE-FLY, *ORNITHOMYIA LAGOPODIS*.

The relation of the grouse-fly, *Ornithomyia lagopodis*, to the grouse has been to some extent a matter of conjecture. Though the grouse-flies often are found clinging to or concealed among the feathers of the birds, the biology of the fly was uncertain, and it was not known definitely whether the flies obtained blood from the grouse or not. Having dissected several hundreds of grouse-flies in an endeavour to find developmental stages of some of the Protozoa infecting grouse, and possibly parasites natural to the fly itself, I append the following notes on the insect, that may be of interest.

Regarding the food of the grouse-fly, the insect sucks the blood of the grouse. Blood in all stages of digestion has been obtained from the gut of the fly. Nucleated red cells of grouse blood, which show no sign of digestion, are found in the red fluid in the crops of recently fed flies taken from grouse, while on a few occasions leucocytes also have been observed. The stomach and particularly the intestine contain blood that is semi-digested and consists almost entirely of cell nuclei.

The blood, especially in the fore-part of the gut, has a peculiar tint, and further, retains its fluidity for a very long time. Examination of the salivary glands of the fly has shown that an anti-coagulin is secreted by them. I have tested the power of this anti-coagulin in delaying the clotting of human blood, using capillary tubes of blood and emulsion, and blowing out the contents at intervals, controls being carefully kept. Blood mixed with emulsion of the salivary glands required nine minutes for coagulation, while the controls, using salt solution, had clotted in six minutes. The intestine of the fly also has anti-coagulin in it. Another member of the *Hippoboscidae*, the sheep ked, *Melophagus ovinus*, also secretes an anti-coagulin. The blood ingested by both flies is prevented from coagulating, and thereby is kept in a more suitable condition for digestion and absorption by the fly.

The peculiar colour of the blood in the fore part of the fly's alimentary canal is apparently to be associated with some action of the anti-coagulin, for an emulsion of the salivary glands of the fly added to human blood caused the latter to assume the same peculiar hue as was noticed in the blood from the crop of the grouse-fly.

A fungus also infests the Malpighian tubes of the fly. The hyphal threads of the fungus rapidly develop rounded masses of spores within sporangia. The sporangia completely fill the

Malpighian tubes, the spores finally bursting out as rounded bodies into the lumen of the gut, and thence pass outside the host. *Melophagus ovinus* contains a similar fungus [see Porter (1910)].

In connection with the fungus, which is common in the grouse-flies, I may say that I have never found flagellates present where the fungus existed, and a similar condition obtains in the sheep-ked, *Melophagus ovinus*.

The grouse-fly, examined as a possible vector of the protozoal parasites of the grouse, yielded rather poor results. However, I have found protozoal vermicules, some without melanin, others doubtfully with a little, in the gut of the fly. These might be stages (cokinetes?) in the life-history of *Leucocytozoon lovati* or *Haemoproteus mansonii*, or of both. There is also the possibility of *Ornithomyia lagopodis* being the transmitter of *Spirochaeta lagopodis*, though I am inclined to suspect *Ixodes ricinus* here, but the whole question of the transmission of the protozoal parasites of grouse is one demanding much more material and very careful investigation.

I also kept a number of the pupæ of the grouse-fly for further investigation, but unfortunately they have not hatched out yet. Dr. Shipley (1909, pp. 321-3) has already published an account of the grouse-fly in which the possible time needed for hatching is discussed, together with much information regarding the adult fly.

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## EXPLANATION OF PLATES LIX.-LXI.

All figures were outlined with the Abbé-Zeiss camera lucida, generally using Zeiss 2 mm. apochromatic immersion objective and compensating oculars 4, 8, 12 (Zeiss). For a few figures Zeiss DD objective and Huygenian ocular 4 were used.

PLATE LIX. figs. 1-16. *Leucocytozoon lovati*. (× 1400.)

From preparations, chiefly heart blood, coloured with Giemsa's stain.  
Magnification: 1400 diameters.

- Figs. 1-3. Young intracorpuseular parasites.
- 4-13. Older parasites in which the host cell is drawn out into horns or processes at either end, and its nucleus displaced.
- 4, 9, 11, 13. Male gametocytes with hyaline protoplasm.
- 5, 6, 7, 10, 12. Female gametocytes with granular protoplasm. Chromatoid granules occur around the poles of many of the gametocytes.
- 14-16. Gametocytes in which much of the host cell is absorbed or discarded, with only slight remains of host-cell nucleus. Figs. 15, 16 from specimens in the spleen. Fig. 14 from the liver. Such parasites, however, are not confined to the internal organs.

## PLATE LX.

Figs. 17-28. *Leucocytozoon lovati*.

- 17-22. *L. lovati* as seen in life, stained with methylene blue. Young parasites, showing formation of tailed processes of host cell. × 1000.
- 23-28. Schizogony of *L. lovati*, as seen in spleen smears from grouse. × 1400. Free merozoites represented in figs. 27, 28.
- 29-40. *Spirocheta lagopodis*, from blood of grouse. × 2500.
- 41, 42. *Hæmoproteus mansonii*. Young parasites in erythrocytes of grouse. × 1800.

## PLATE LXI.

- Figs. 43-50. *Trichomonas eberthi* and *Monocercomonas*.  $\times 1400$ .  
 43-46. *Trichomonas* forms from cæcum of grouse.  
 47-48. *Monocercomonas* forms. Fig. 47 intermediate form.  
 49. Dividing *Trichomonas*.  
 50. Encysting *Trichomonas*.  
 51-57. *Spirochæta lovati* from the cæca of grouse.  $\times 1700$ .  
 58-65. *Amœba (Entamœba) lagopodis* from intestine and faeces of grouse.  
 58, 59, 61, 62, 63. Amœbæ.  $\times 500$ .  
 60. Amœba which has assumed a pyriform shape.  $\times 750$ .  
 64-65. Encysted amœbæ.  $\times 1000$ .

3. Experimental Studies on Avian Coccidiosis, especially in relation to young Grouse, Fowls, and Pigeons. By H. B. FANTHAM, D.Sc. Lond., B.A. Cantab., A.R.C.S., F.Z.S., Christ's College, Cambridge, Assistant to the Quick Professor of Biology in the University of Cambridge; Protozoologist to the Grouse Disease Inquiry.

(Plate LXII.\* and text-figure 66.)

[Received April 5, 1910.]

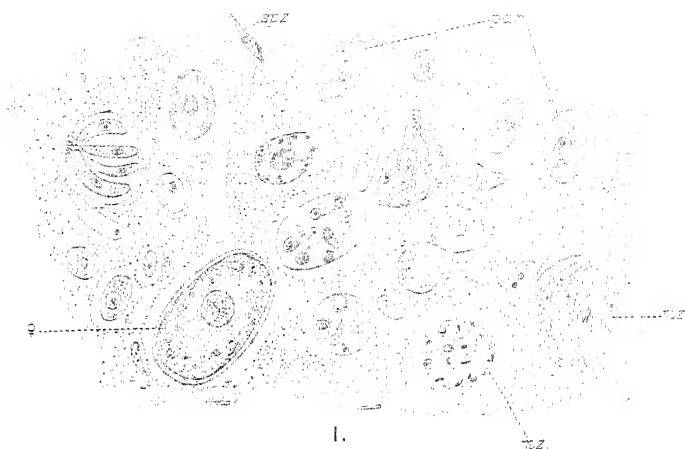
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## I. INTRODUCTION.

Protozoal parasites are highly specialised animalcules which live in intimate relation with the hosts they infect. While many of the Protozoa are capable of living in one host only, there are others which are under suspicion of infecting several species of higher organisms as host, and of not being so limited to one host as was formerly believed. One test for the specificness of any protozoal parasite is that it fails to develop in any animal other than its special, natural host, and merely perishes when inoculated or otherwise introduced into any other animal. In order to test the specificness of the coccidian parasite of the grouse, experiments were made, with the result that the *Coccidium* pathogenic to young

\* For explanation of the Plate see p. 722.



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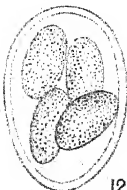
9.



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14.

H.B. Pantnam del.

E. Wilson, Cambridge.

AVIAN COCCIDIOSIS.



grouse and responsible for the dwindling of the broods, particularly in the spring and early summer, was found to be equally injurious to healthy young fowls and young pigeons. Healthy grouse chicks also were experimentally treated by administering food mixed with small quantities of infected faeces from other grouse suffering from coccidiosis, and fatal results ensued.

The results set forth in this memoir are those obtained from one season's work only, to which my investigations were limited.

## II. EXPERIMENTAL METHODS.

The birds used in experimental coccidiosis were grouse chicks, fowl chicks and young pigeons, all of which were initially healthy. Coccidian oöcysts (Pl. LXII. figs 4, 5) contained in caecal droppings from infected grouse were allowed to develop spores to some extent by being thinly spread in Petri dishes and covered in order to prevent complete drying. Under these conditions the spores (figs. 6, 7) developed in two to three days at summer temperature. The faeces so prepared were then administered to the healthy young birds.

(A) *Grouse Chicks*.—As these birds are somewhat wild, even though bred in captivity, a rapid feeding method was adopted. Some of the partly dried faecal matter was taken up on a spatula and inserted directly into the mouth of the bird. Rather large quantities were given as first doses, but if infection was not fairly rapidly brought about the dose was repeated. The caecal droppings of treated chicks were collected each morning, for these soft droppings are more abundant during the night than they are during the day, and in the early morning there is a better chance of obtaining excrement free from soil. Examination of faeces collected in the evening was sometimes made.

The grouse chicks were kept on the experimental ground at Frimley, and the feeding experiments were conducted by Dr. E. A. Wilson, to whom I tender my best thanks. Samples of the faeces of the birds were sent to me daily.

(B) *Fowl Chicks and Young Pigeons*.—A method of feeding similar to that used for grouse chicks was employed with fowl chicks and young pigeons (squabs). These experiments were conducted by me at Cambridge. The chicks used were from incubated eggs, the eggs having been carefully cleansed antiseptically before incubation. Caecal droppings containing oöcysts were administered directly to the birds. Very small daily doses were used for several days and then none for a couple of days, and so on. This method of administering oöcysts was quite effective and had the advantage of reproducing somewhat the condition of wild grouse on the moors, where intermittent ingestion of oöcysts with food or drink occurs.

One experiment was performed in which a single dose only had a fatal effect on a fowl chick.

Droppings containing oöcysts in different stages of development



(figs. 4-7) were also used. When the oöcysts contained developed sporocysts the onset of coccidiosis was more rapid.

Again, I have found coccidian oöcysts in the water of burns at which grouse chicks drink and also in dew collected from the heather on the moors (fig. 8). Grouse chicks, then, can acquire coccidian oöcysts by way of their drink. To show this method of infection experimentally, a healthy fowl chick was supplied with water containing coccidian oöcysts. This bird also became infected with coccidiosis.

Control birds were most carefully kept. These were supplied with food and drink exactly as were the treated birds, and kept under the same conditions. Examination of their faeces was made twice daily, and careful search was made for oöcysts as the possibility of natural coccidiosis of both fowls and pigeons\* was well recognised and most carefully guarded against. Control birds invariably were healthy and made more rapid progress in growth than did the subjects of the experiment.

In every instance I most carefully compared the results obtained experimentally with the cases of natural coccidiosis in grouse chicks that I investigated at Killin (by the courtesy of Lord Lovat) and in other cases obtained from Perthshire, Dumfriesshire and Yorkshire.

Some authors have given the name *Coccidium cuniculi*† to the parasite of birds, thereby identifying the coccidium of birds with that of rabbits. Having had the opportunity of obtaining fresh material from rabbits dying rapidly of acute coccidiosis, I fed a healthy young pigeon directly with oöcysts of *C. cuniculi*. At first oöcysts were voided by the pigeon, then none were found in the faeces and no symptom associated with coccidiosis appeared at any time. The first oöcysts voided were merely those supplied to the bird which had passed unchanged through its alimentary tract. Though this pigeon received several doses of the oöcysts of *Eimeria* (*Coccidium*) *cuniculi*, it never developed coccidiosis, and the post mortem examination made immediately after killing the bird showed a perfectly normal condition of every organ. I consider that these experiments show conclusively that *E. arium* and *E. cuniculi* are distinct species of *Eimeria* and are not identical. There are also morphological differences between the two, chiefly of size (*E. arium* is the smaller).

### III. SYMPTOMS OF COCCIDIOSIS.

The symptoms of grouse suffering from natural coccidiosis and those of grouse, fowl chicks, and pigeons, in which the disease has been artificially induced, are identical. The symptoms that have been noted in the case of the birds examined may now be stated.

\* Through the courtesy of a friend I was able to examine Coccidian oöcysts from a pigeon suffering from natural coccidiosis. On Pl. LXII. fig. 13 is drawn a cyst of this *Coccidium* (*C. pfeifferi* of Labbé). It is spherical, about  $17\mu$  in diameter.

† The correct name of this parasite is *Eimeria stieda* Lindemann.

Chicks after ingesting coccidian oöcysts become far less active in their movements as a rule. The first noticeable feature is the drooping of their wings and a habit of constantly looking downwards. The birds stand about more than normal birds and their calls are more plaintive.

While fowl chicks and pigeons appear to mope, their appetite is increased, and chicks experimentally infected with coccidiosis eat far more greedily than the control birds. They also drink considerably more. In spite of the increase in the amount of food consumed, the birds rapidly get thinner, the muscles of the breast and legs showing this to a marked degree. Throughout the progress of the disease the growth of the affected birds is much retarded.

It was necessary to feed infected young pigeons by hand, for even when they reached practically adult life they failed to feed themselves, merely thrusting their heads into the food offered them, without attempting to swallow any of it.

Several breeds of fowl chicks were used in experimental coccidiosis and each lost weight steadily till death occurred. The loss of weight of one pure bred Leghorn chick was very noticeable. It was first fed with coccidian oöcysts when six weeks old. It and its control bird were then of equal weights ( $7\frac{1}{2}$  oz.). Two months later the infected chick died, its weight at death being 5 oz., while the weight of its control on the same day was 1 lb. 6 oz.

Sample weights of other experimental birds are given below :—

BIRD.	Weight of Infected Bird.	Weight of Control Bird.	Difference in Weights.	Remarks.
Grouse chick A .....	4 oz.	$5\frac{1}{2}$ oz.	$1\frac{1}{2}$ oz.	Dosed once when 11 days old. Killed in extremis when aged 6 weeks. Died, aged 10 weeks.
Grouse chick B .....	$4\frac{1}{2}$ "	7 "	$2\frac{3}{4}$ "	
Grouse chick C .....	$6\frac{1}{2}$ "	9 "	$2\frac{1}{2}$ "	
Minorea hen.....	3 lb. 2 oz.	5 lb. 2 oz.	2 lb. 0 oz.	Died, aged 6 months.
Plymouth Rock cock ..	4 lb. 8 oz.	6 lb. 5 oz.	1 lb. 13 oz.	Killed, at acute stage of disease.
Cross-bred Leghorn.....	4 lb. 10 oz.	5 lb. 4 oz.	10 oz.	Chronic.
Pigeon .....	$9\frac{1}{2}$ oz.	12 oz.	$2\frac{1}{2}$ oz.	Died, aged 11 weeks.

NOTE.—The three fowl chicks were first treated with Coccidian oöcysts when aged 3 weeks. Another fowl chick fed with Coccidian oöcysts when aged 1 day, died when 9 days old. The pigeon squab was dosed first when aged 9 days.

Another instance of loss of weight resultant on coccidiosis was seen in the case of a pure bred female Leghorn chick which was attacked when seven weeks old by coccidiosis after drinking water fouled with coccidian oöcysts. This bird became a chronic, and

when adult weighed 4 lb. 3 oz., while its sister bird that acted as control weighed 5 lb. 4 oz.

Besides loss of weight the infected birds become anæmic. The cere, comb, and wattles become much paler and the blood-vessels beneath the wing also look pale. The head appendages gradually become more and more pale as the disease progresses and finally acquire a peculiar bluish tinge. This tint also is shown by the eyelids and ears and the legs are affected though to a less extent. The feathers on the head tend to fall off so that the forepart of the head and the region round the bill become almost bald, and the bird presents a very peculiar appearance, owing to the bluish coloration. Leg weakness was present in several cases.

The plumage of the infected birds is affected in regions other than the head, and the quills are less rigid than in normal birds. The feathering of the legs is ragged and the sheen on the neck and tail-coverts is not so well developed, while the replacement of nestling down by ordinary feathers is much retarded in diseased birds.

During the progress of coccidiosis the birds sometimes develop much mucus and a very offensive "breath," a smell of sulphuretted hydrogen being noticeable. Both sticky mucus and smell disappear as a rule in a few days, but may recur.

While birds suffering from coccidiosis feed greedily, internal digestive troubles occur and the fæces voided by the birds are very fluid, the condition being that of diarrhœa. The cæcal droppings are the more noticeable, and they contain many resistant cysts (oöcysts) (figs. 4-8) of *C. avium*. Both sportsmen and keepers have noted that diarrhœa is a marked symptom of "grouse disease." Examination of soft droppings daily shows the relative numbers of oöcysts present and may be a rough gauge of the intensity of the infection\*. In good health the cæcal droppings are of firm consistency and olive-green to brown in colour. When coccidiosis is slight, the fæces become softer and brownish yellow. In acute cases the excrement is almost fluid and the birds void sulphur-yellow fæces with a heavy, fetid odour. Fatty matters may be present in the cæcal contents.

A day or so before the death of the infected bird the slimy, mucilaginous discharge recommences, ooze coming from the beak, nares, ears and eyes. Examination of this liquid by the microscope shows the presence of oval coccidian oöcysts (cf. Pl. LXII. figs. 4-8), all of which show the characteristic cyst-wall within which is a single uninucleate mass of protoplasm. The mucus also contains some shed epithelial cells in which occasionally macro- and micro-gametes may be found. The ooze from the eyes and beak chiefly contains oöcysts which may be due to regurgitation from the crop just before death. However, it

\* It should be noted that in severe cases of duodenal coccidiosis, merozoites may be found free in the gut-contents and fæces of infected birds when no oöcysts are present.

should be noted that while mucous discharge is common, it is not an invariable feature of coccidiosis.

Death from coccidiosis appears to be sudden. Some of the experimental fowl chicks were feeding greedily an hour before death, though death was almost expected from the great emaciation and "bluish" appearance of the birds for some days previous to the actual decease. All infected corpses should be burned, *not* buried.

#### IV. INTERNAL ORGANS.

Detailed examination of diseased birds shows that coccidiosis of fowls, pigeons and young grouse is confined chiefly to the digestive tract, and so is unlike the coccidiosis of the rabbit where both the liver and the gut may be affected.

Dead chicks have shown oval coccidian oöcysts (text-fig. 66, p. 714) in the discharge from the nostrils. Scrapings from the soft palate, trachea and oesophagus of diseased birds have shown the presence of oöcysts embedded in mucilage. Possibly the oöcysts may be regurgitated from the gizzard or intestine. Oöcysts are occasionally present in the crop and gizzard, mixed with crushed food, having been probably taken up with the food.

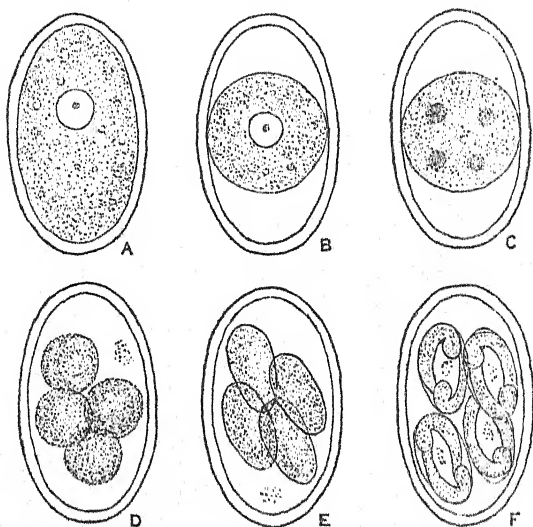
The intestine is more highly parasitised than any other part of the alimentary tract. The oöcysts (Pl. LXII. figs. 7, 8, 11, 12), which show much variation among themselves, are softened by the pancreatic juice, the four sporocysts (figs. 9, 10) emerge and from each of them two active, motile sporozoites or germs come out and proceed to attack the epithelium of the duodenum. Having penetrated the epithelium (fig. 1) they become round, grow and produce individuals, destined to divide and give rise to a barrel-shaped mass of active daughter germs, the merozoites (fig. 1, *mæ*). These merozoites separate from one another and infect fresh epithelial cells, the whole mucous membrane being soon badly infested, and becoming reduced to an almost structureless mass (fig. 1). Owing to heavy infection in the duodenal epithelium, death of the young grouse may occur. However, in many cases, some of the merozoites pass into the lumen of the gut and reach the cæca, the tissues of which are similarly mutilated. As far as my experiments go at present, the full period of schizogony would appear to be from 4 to 5 days, as judged by the appearance and general moping of the birds.

After several generations of merozoites have been produced, the power of the host to provide food for the parasite fails, and consequent on this, the latter begins to make preparation for extra-corporeal life and produces large, granular forms, which are female mother cells or macrogametocytes (fig. 1, ♀) and somewhat smaller, less granular ones which are microgametocytes (fig. 2, ♂). Each macrogametocyte gives rise to one passive macrogamete or female element (fig. 1), while each microgametocyte gives rise to many minute, motile microgametes, the male elements (fig. 2). Fertilisation (fig. 3) occurs through a micropyle left in the wall

with which the macrogamete invests itself, and the fertilised oöcyst so produced, passes out through the much damaged epithelium into the lumen of the gut and thence to the outside. The epithelium of the duodenum and caeca is sometimes entirely denuded by the action of the many parasites that infest it, and the sub-mucosa also is sometimes infected by the *Eimeria*.

The contents of the oöcyst, at first filling the interior (text-fig. 66, A), gradually contract (text-fig. 66, B) towards the centre, or occasionally towards one pole, and then divide (text-fig. 66, C) into four round masses (text-fig. 66, D) known as sporoblasts. Each sporoblast becomes an oval sporocyst (text-fig. 66, E) while still within the oöcyst, and within each ripe sporocyst two sporozoites or germs are developed. Consequently each oöcyst gives rise to eight sporozoites (text-fig. 66, F).

Text-fig. 66.



Figures A-F.

Stages in the development of the oöcysts of *Eimeria avium*, as seen in fresh preparations.

- A. Oöcyst (encysted zygote) with protoplasm completely filling it.
- B. Older oöcyst with zygote contents forming a central sphere. Many such cysts are found in infected caeca and infected faeces of grouse.
- C. Oöcyst with four nuclei, about to form sporoblasts.
- D. Oöcyst with four round sporoblasts.
- E. Four ovoid sporocysts within oöcyst.
- F. Fully mature oöcyst with four sporocysts, each containing two sporozoites.

A certain amount of variation, as exhibited by the oöcysts of *E. avium*, has been noticed by Morse (1908) in the coccidian parasite of "white diarrhea" of fowls, where the oöcysts are round to oval, and from  $12\mu$  to  $25\mu$  in diameter. The oöcysts of *E. avium*

in grouse, which is identical with the parasite found in "white diarrhoea" of fowls, also vary among themselves. Usually the oöcysts are oval (figs. 4-8), but a series of varying sizes and shapes can readily be found (figs. 8, 11, 12, 14), while round oöcysts also occur (fig. 11). The exact shape and size of the oöcyst is a factor of the space in the cell available for the development of the macrogamete, and should not be insisted upon as a specific character, for where many parasites are aggregated together in a limited area of epithelium, the macrogametes and oöcysts are small, while in areas of the gut but poorly parasitised, large oöcysts preponderate. Nutrition of the parasite has obviously a great influence on both its size and its propagative power.

In some cases the gut-wall is extremely thin and tender; in other birds this effect is not marked. Inflammatory patches may be seen at intervals, particularly in the caeca, and the caeca usually are enlarged. At the ileo-caecal junction, where a recurrence of schizogony and sporogony occurs, much degenerated epithelium is present in the gut contents, and this epithelium contains both schizonts and gametocytes.

The large intestine of chicks infected with coccidiosis sometimes shows inflammatory patches and blood may be present in the rectal contents. The rectum itself seems rarely to be attacked by *E. avium*, though its contents usually contain oöcysts.

The kidneys, spleen, liver, and gall-bladder of birds suffering from coccidiosis never contained *Eimeria*, though the spleen and gall-bladder were sometimes enlarged. Examination of the generative organs has shown no stage of *E. avium* so far, though it is possible that eggs may become contaminated during their passage through the cloaca of the mother. The young chicks then might be hatched in contact with infectious material, and so acquire coccidiosis early in life. Eight days old grouse chicks were the youngest naturally infected chicks that I examined. The period of 8 to 10 days is the one determined roughly by my experiments as being required for the complete developmental cycle of *E. avium* in fowls and pigeons, from the time of ingestion of the oöcysts to the excretion of the maximum number of oöcysts of the second generation.

Many bacteria are present naturally in the gut of the grouse, and their active movements can be well seen, especially in the caecal contents of freshly killed grouse. Examination of sections of the gut of the grouse, especially of sections stained with iron-haematoxylin and iron-haematoxylin followed by van Gieson's stain, reveals the presence of numerous bacteria which are present, not only in the lumen of the gut, but forming a layer along the striated edge of the columnar epithelial cells, and also are found in lesions left by the outward passage of gametes and merozoites. These bacteria may have a harmful effect on the tissues invaded, and there is evidence to show that they gain access to the tissues very early, the sporozoites and merozoites acting, in fact, as inoculating needles, whereby the injurious bacteria are passed into the tissue of the gut, whence, by way of the blood and lymph,

they can reach other organs. Further, the denudation of the epithelium of the gut allows of easy entry of bacterial agents of infection.

In connection with the action of bacteria in the disease of fowls known as "white diarrhoea," there are two opposing views. Morse (1908), working in America, has investigated white diarrhoea in fowls and other birds and always found intestinal coccidiosis. Hadley (1909), also working on the subject, found not only intestinal but also hepatic coccidiosis in fowls suffering from white diarrhoea. Morse notes the presence of bacteria in the gut, and thinks that they may gain access to the system on account of the denudation of the gut epithelium. Rettger (1909), on the other hand, considers that white diarrhoea is due entirely to a bacterium, *Bacterium septicemice gallinarum* or *Bacterium pullorum*.

Probably both of these conflicting views are right as far as they go, but separately they may only partially explain the cause of "white diarrhoea." Drs. Cobbett and Graham Smith, of the Grouse Disease Inquiry, have shown (1910) experimentally that Bacteria may be inoculated by means of coccidia, and find their way into the internal organs probably by way of the portal vein. The agency of parasitic worms and coccidia in causing lesions of the mucous membrane through which harmful bacteria may enter, is of far-reaching importance and probably of wide application in the elucidation of certain intestinal diseases.

Morse's paper gives much valuable information regarding treatment of coccidiosis and brief notes on intestinal coccidiosis of various birds. Game birds other than grouse are susceptible to coccidiosis, for M'Fadyean reported coccidiosis in pheasants in 1893-4. At the time of correcting proofs of this article I am engaged in investigating coccidiosis which is causing the death of many young pheasants in various parts of England.

The onset of sporogony of *E. avium* means either the recovery or the death of the infected chick as a rule. When the oöcysts pass out from the body of the host, the epithelium of the gut may be able to recover itself, when the bird gradually increases in weight and makes partial or entire recovery. This recovery is sometimes aided by infiltration of connective tissue into the lesions. If, however, the infection has been heavy, the epithelium cannot regenerate itself and the bird becomes exhausted and dies.

#### V. RELATIVE RESISTANCE OF DIFFERENT BREEDS OF FOWLS AND PIGEONS TO COCCIDIOSIS.

Young chicks are far more susceptible to coccidiosis than adult birds\*. Very young fowl chicks (up to 8 days old) die in a few days after being fed with coccidian oöcysts. Chicks first dosed with cysts when 14 days old do not succumb so readily; they may live

\* Old birds may become chronics and thus infect the moors. In this connection infected foster mothers in pheasant-rearing may be dangerous.

for some weeks or some may become chronics, when daily examination of their faeces shows periodic small crops of oöcysts.

Older chicks are more likely to recover from coccidiosis. For example, a grouse chick aged 13 weeks was fed on oöcysts, and when killed 3 weeks later very few coccidia were observed. Again, a young grouse which had been picked up dead on the moors in Inverness-shire was received on Sept. 15, 1909. In its caeca numbers of both coccidian oöcysts and *Trichostrongylus pergracilis* were found. The bird had probably survived an attack of coccidiosis and in its weakened condition had fallen a victim to strongylosis.

Different breeds of fowls have varying powers of resisting coccidiosis. Pure-bred Leghorn and Minorca chicks died from the disease in a comparatively short time. Plymouth Rock chicks were attacked quickly but had greater resisting powers than pure Leghorns or Minorcas. Cross-bred Leghorns were far more resistant to the disease than the pure-bred birds.

Regarding pigeons, fantails are more susceptible than the ordinary pigeons, though squabs of any variety seem easily attacked and overcome by coccidiosis.

#### VI. THE DISSEMINATION OF COCCIDIOSIS OVER TRACTS OF COUNTRY.

Coccidiosis outbreaks spread with fair rapidity, but though many birds in one locality become diseased, yet adjoining estates may be free. Epizootics of coccidiosis also disappear very quickly.

Infection has been shown experimentally to be due to the ingestion of oöcysts (cysts), either by way of the food or drink. Coccidian cysts may occur on the heather and in the tarns and pools from which the grouse drink, as before mentioned.

When faeces of infected chicks are voided, the caecal or soft droppings are heavily loaded with cysts, and not only do they foul the ground, heather, and water in their vicinity, but when dried, the powdery material produced may be disseminated by the wind, and so oöcysts and their contained sporocysts are distributed over comparatively large tracts of country.

But other methods of producing richer local infections may be partly due to insects. The agency of insects such as dung-flies has been observed in nature and also demonstrated experimentally.

*Scatophaga stercoraria*, the dung-fly, commonly occurs on grouse moors. The eggs of the fly are laid in faeces and hatch out there. The larvæ are large and somewhat active. They feed on the faeces of grouse, which faeces may be infected with coccidian cysts. Dissection of such larvæ has shown the presence of oöcysts within their guts. When isolated larvæ were first well washed and then allowed to defæcate on a slide, the preparation of the faeces showed oöcysts when examined microscopically. Some of the pupæ also contained coccidian spores in their guts. The freshly hatched



flies examined rarely showed spores, but as they proceed almost at once to ingest faeces, they rapidly become agents for distributing the spores. Dung-flies allowed to hatch out in the faeces of infected grouse always contained coccidian oöcysts in their alimentary canal and faeces.

Laboratory experiments were made with the blow-fly, *Musca vomitoria*. Eggs taken from the body of the parent fly were allowed to hatch out in faeces of an infected grouse chick. The larvæ greedily ingested the cysts which passed practically unaltered through their bodies. Some of the larvæ which pupated were washed very carefully and then dissected. They contained coccidian spores. Adults were fed on the infected material and oöcysts were voided in their excrement. The spreading of young flies, hatched infected, and of older ones that have fed on infected material, may aid, then, in the dispersal of coccidiosis.

While experimental evidence of the action of *Scatophaga stercoraria* and *Musca vomitoria* has been afforded in the laboratory, this is merely confirmatory of what may occur on some moors. Here on Scots firs, heather and moss, numbers of flies are found, and dung-flies are known wherever grouse droppings are to be found. The trail of birds can be tracked to some extent by the coprophagous flies, while lines of infection are produced by the birds as they pass down by small paths to their drinking places.

It may be of interest to note that houseflies (*Musca domestica*) have been shown experimentally to ingest coccidian oöcysts.

To summarise, wind and rain acting on infected faeces are probably the principal agents in dispersal, while the feeding habits of *Scatophaga* and other flies form subsidiary means of spreading the disease.

## VII. DURATION OF VITALITY OF COCCIDIAN OÖCYSTS.

### (a) When the Oöcysts are kept in water or very moist.

Much moisture is present on many moors, and faeces of infected chicks contain coccidian spores which not only get washed into the soil, but also into tarns, etc., at which grouse drink. It was, therefore, of some importance to determine the time required for the degeneration of the resistant spores of the parasite when in water.

Coccidian oöcysts with undifferentiated contents were placed in water, kept at about 20° C. (July temperature), the water being replaced as required, to avoid evaporation effects. Ordinarily, the oöcysts develop sporocysts very rapidly—in 2 to 3 days. In the case of cysts kept in water, 9 days elapsed before much change was noted. At the end of that period, a few oöcysts showed differentiated protoplasmic masses, and still fewer showed four sporocysts. Two days later many more oöcysts contained four sporocysts, and this progressive development continued for some days. Little signs of degeneration were seen until about the 40th day, when some showed signs of gas bubbles in their interiors. Others, however, had completed their development, and their four

sporocysts, apparently unharmed, were set free into the liquid. By the 50th day, practically all oöcysts had either matured or degenerated, and the sporocysts had begun to degenerate.

From the above experiment, the conclusion is that the development of oöcysts and sporocysts is delayed by the presence of much moisture, but that the power of infection is retained for a long time by means of the sporocysts.

Very damp air has similar effects.

( $\beta$ ) *When Fæces are merely kept and allowed to dry on the outside.*

When freshly voided soft droppings of grouse containing coccidian oöcysts are allowed to dry, the oöcysts in the surface layers rapidly develop sporocysts, the inner ones remaining unaffected.

Fæces kept *en masse* in covered dishes for as long as twelve months have retained the power of infecting birds, as I have been able to show experimentally. Such material contains undifferentiated oöcysts still, while its outer layers mainly contain oöcysts with four sporocysts within them.

( $\gamma$ ) *Development under Different Conditions of Temperature.*

For experimental purposes, it was sometimes necessary to delay the development of sporocysts. This was easily done. The oöcysts in fæces were transferred to a chamber kept at 10° C., having been previously kept at 15° C. This change was sufficient to delay all further development for a considerable time. Smaller changes of temperature also arrested the development of sporocysts, though the effect naturally was not so marked.

Changes of temperature and moisture on the moors may explain the occurrence of occasional outbreaks of disease after all disease seems to have disappeared. Moisture and coolness retard the development of certain oöcysts for a considerable time, during which period the disease disappears. A return of conditions favourable to the *Coccidium* then ensues, rapid development of sporocysts occurs and a fresh outbreak of disease is reported.

### VIII. EFFECTS OF CERTAIN REAGENTS ON COCCIDIAN OÖCYSTS.

Certain experiments were made with a view to finding a means of destroying oöcysts without killing all other forms of life.

This is not an easy matter. While such strong re-agents as caustic potash will slowly dissolve the oöcysts, their application is not practicable on grouse moors.

*Salt* produces plasmolysis in the end, but the process is rather slow, and the salt is too readily dissolved in dew and rain, and so merely soaks into the soil\*.

\* However, in this connection see Hammond Smith, "The Field," Aug. 20, 1910, Suppl. p. viii.

*Quick-lime* destroys the oöcysts and sporocysts. It also causes the faeces to cake, thereby preventing scattering of the spores. It is somewhat doubtful whether lime could be applied on a large scale. It might be somewhat harmful to the feet of the birds, apart from the difficulty of distributing it over large areas. Where the area of infection is small, it is probable that the application of lime to the soil would be of service. My experiments on a small plot of heather at Cambridge have shown that small quantities of lime dressing are not detrimental to heather.

*Gas lime* and *slaked lime* also are useful, but each is open to the same objection as quick-lime. Lime in one form or another certainly seems to have the best and most rapid action on coccidian oöcysts of any reagent that I have tried.

*Salicylates*.—Salicylic acid and sodium salicylate act rather slowly on coccidian oöcysts when mixed with them. Both chemicals tend to deliquesce, and the faeces mixed with them remain fluid for a longer period than they otherwise would. The oöcysts become wrinkled and ultimately destroyed, but the contents take longer to degenerate than when lime is used.

*Ferrous sulphate*.—Copperas or green vitriol is useful to some extent in destroying coccidian oöcysts, but like salicylates it is somewhat slow in action. A dusting of ferrous sulphate on the moors would probably be useful, for the combined iron present might be taken up in small quantities by grouse and, by acting as a general tonic, might enable the birds to resist coccidiosis the better if they became attacked. Ferrous sulphate in the proportion of 10 grains to the gallon of drinking-water has been found of service by the writer in the treatment of coccidiosis in young fowls and young pheasants. Some keepers and breeders, at my suggestion, have used *catechu* in the drinking-water with success.

*Sodium nitrate*.—Nitrate of soda mixed with faeces destroyed the contents of the oöcysts after some time, but the length of time required for its effective application would militate against its use on a large scale.

In my experiments at Cambridge, three portions of infected faeces were mixed with equal quantities of lime, sodium salicylate, and ferrous sulphate respectively, and were kept in open dishes, exposed to the action of the weather. The results obtained may be shortly given.

In the case of *lime*, the faeces rapidly formed a caked mass. In a fortnight the oöcysts were shrunken and wrinkled, and some showed cracks. At the end of three weeks, the cysts were more broken up and the contents largely disintegrating, while after a lapse of two months, there was a difficulty in finding spores at all. Bacteria were not found after lime treatment, and there was only a slight faecal odour noticed.

*Sodium salicylate* added to faeces rapidly deliquesced, in fact, the mixture was quite liquid in less than three hours. After a

fortnight's interval, the cysts appeared to be slightly shrunken, while faecal odour was noticeable. A month later, the oöcysts were more shrunken and a few free sporocysts were found, while ten weeks after treatment, a slight smell was still perceptible, and the oöcysts present were shrunken and showed oily contents.

*Ferrous sulphate* (copperas) had much the same effect as sodium salicylate, but did not deliquesce. Though its action at first seemed to be rather less effective, it secured the same result ultimately.

#### IX. CONCLUDING REMARKS.

The ravages of coccidiosis among grouse chicks may be underestimated on the moors, since the tiny corpses of the birds lie hidden among the heather.

While it is relatively easy to take preventive measures in the case of coccidiosis in fowls, it is most difficult to take active measures in the case of grouse. The remedy of heather burning is drastic and coccidian spores, which are present in the tract burnt, are then destroyed. However, heather is rather slow-growing, and so heather-burning, while efficacious, is somewhat restricted in its area of application. Lime dressing is destructive to spores of coccidia, and could probably be utilised in the case of limited outbreaks of disease among grouse chicks. The effect of lime on the heather on the moors should first be carefully investigated on a large scale (see p. 720). Any condition tending to raise the general vitality of the birds also makes them much more resistant to disease. An abundant supply of healthy young heather, by raising the general standard of health of the birds, is probably one of the best safeguards against the insidious disease, coccidiosis.

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## EXPLANATION OF PLATE LXII.

All figures outlined with Abbé camera lucida, using Zeiss 2 mm. apochromatic lens.

Figs. 1, 2, 3 from stained (hæmatoxylin) sections of gut of grouse chick infected with coccidiosis.  $\times 1500$  approximately.

Figs. 4-14 from fresh preparations.  $\times 1000$ .

Figs. 1, 2. Section of gut showing parasites.

*par.* = parasite.

*spz.* = sporozoite (infecting germ).

*mz.* = merozoite (daughter form).

$\sigma$  = microgametes (male elements) attached to microgametocyte ( $\sigma$  mother cell).

$\phi$  = macrogamete (female), with thin cyst around it.

3. Fertilisation of large macrogamete by minute microgamete. Only one male element penetrates, the others remain on the outside and degenerate.

4, 5. Oöcysts, characteristic of fresh faeces.

6, 7. Oöcysts with four developing sporoblasts inside, first round, then ovoid.

8. Mature oöcyst containing four sporocysts, each with two sporozoites, from caecal droppings taken from the moors.

9, 10. Free sporocysts (spores) from infected faeces. In the sporocyst represented in fig. 10, which is pointed at one end, the sporozoites are about to emerge.

11. Round cyst, as found in droppings of grouse or fowl chicks.

12. Somewhat egg-shaped cyst, with four sporoblasts (young spores).

13. Cyst of *Coccidium pfeifferi* (Labbé) from a pigeon infected with natural coccidiosis.

14. Cyst from faeces of a pigeon fed on infected grouse faeces.

4. Observations on the Blood of Grouse. By H. B. FANTHAM, D.Sc.Lond., B.A.Cantab., A.R.C.S., F.Z.S., Christ's College, Cambridge, Assistant to the Quick Professor of Biology in the University, Protozoologist to the Grouse Disease Inquiry.

[Received April 5, 1910.]

(Plate LXIII.\*)

## I. INTRODUCTION.

The elements of the blood of birds are very different from those of mammals, and while much is known of the histology of mammalian blood, the investigation of the blood of birds has hitherto been very limited, and very little indeed is known of the subject. Such literature as is available on avian blood is, unfortunately, largely contradictory, and the few illustrations relating to the same have not solved entirely the difficulties connected with the cellular elements of the blood of birds.

The portions of the subject that have been most adequately dealt with are those relating to certain pathological conditions, fowl cholera and fowl typhoid, occurring in domestic fowls, and those relating to normal fowls' blood. In connection with both

\* For explanation of the Plate see p. 731.



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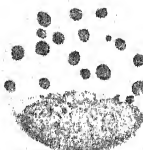
14.



15.



16.



17.



18.

W. L. Palmer, del.

W. L. Palmer, del.

BLOOD CELLS OF BIRDS.  
CHIEFLY OF GROUSE.



these sets of observations there are wide discrepancies between the results obtained by different investigators, and much confusion has arisen therefrom.

The different results obtained by various investigators are partly explicable, for the constitution of the blood of birds may vary among individuals of the same species. Also there are differences due to age and sex, while the conditions under which the investigations are made have some influence on the result.

The chief difficulties of manipulation for the investigation of the blood of such birds as grouse are the rapidity with which coagulation occurs, and the rapid alteration and disintegration that often follows the death of the blood elements. The great rapidity of the onset of degeneration in the leucocytes is such that extreme accuracy in counts of these cellular elements is not easily obtained, and the numbers of erythrocytes and leucocytes found in different series of counts consequently bear a varying relation one to another in apparently normal birds, even when the factors noted in the preceding paragraph have been considered. Nevertheless, the correlation of the numbers and condition of the blood-elements, particularly of the leucocytes, with the occurrence of specific protozoal and helminthic parasites, renders an examination of the blood a most useful adjunct in investigating somewhat obscure diseases. Several protozoal parasites [see Fantham (1910)] are present in grouse, both in the blood and in the gut, and the condition of the bird's blood can be correlated with the presence of some of the individual parasites.

## II. METHODS.

Blood taken from a wing vein was used in the case of living birds, of which twelve were thus examined. In the case of freshly killed grouse, blood taken directly from the heart was employed. The usual methods and precautions were followed in securing suitable drops of blood for examination.

Hayem's fluid was used as a diluent for counting the red cells of the blood, while Toison's fluid was used in the case of the leucocytes.

The Thoma-Zeiss haemocytometer was employed. The disc of the counting chamber was ruled according to Zappert.

A dilution of at least 200 or 250 was found to be necessary for counting the red cells, and a dilution of 20 to 25 was absolutely necessary in counting the leucocytes. Sometimes a dilution of 100 was taken in counting the leucocytes, and this greater dilution was often preferable.

For differential leucocyte counts blood smears were made on both cover-slips and slides, especially the former.

The stain generally used in making preparations for differential counting was that of Jenner. Occasionally Giemsa's stain was employed.



### III. THE CELLS IN THE NORMAL BLOOD OF BIRDS, ESPECIALLY GROUSE.

The elements present in the blood of normal grouse may be grouped as:

- (a) Erythrocytes.
- (b) Leucocytes.
- (c) Thrombocytes.

The leucocytes are further subdivided, and may be grouped as mononuclear, polymorphonuclear, and eosinophile leucocytes, and lymphocytes. Mast cells, which are markedly basophile, are also present. Erythroblasts also may be encountered. These forms may now be considered separately.

(a) *Erythrocytes*.—These are the most abundant elements in the blood. The erythrocytes or red blood corpuscles are oval in contour (Pl. LXIII, fig. 1). They possess a well marked oval nucleus, centrally placed. The erythrocytes of grouse are about  $11.5\text{--}12\ \mu$  long by  $7\text{--}7.5\ \mu$  broad. In fresh preparations the cytoplasm of the red cells of healthy grouse is practically homogeneous, or but very faintly granular. Stained preparations give the same results. It is rare for large granules, chromatoid granules, or vacuolations to be present in the red cells of healthy birds. The nucleus stains deeply, and shows a well-marked chromatic meshwork with small net-knots upon it at intervals.

The red cells of various birds are much the same. There may be slight differences in size and shape. In figs. 2 and 3 are depicted stained specimens of the red cells of the pigeon and fowl respectively, from which it will be seen that the erythrocytes of the pigeon are slightly narrower than those of the grouse and fowl, and somewhat less rounded at the ends.

The number of red cells of grouse varied from 3,600,000 to 5,800,000 per cubic millimetre, averaging 4,300,000 per c.mm. These figures result from blood-counts of 50 birds.

The number of red cells is apparently higher in cock grouse (*e. g.*, 4,400,000 per c.mm.) than in hen grouse (*e. g.*, 3,800,000 per c.mm.).

(b) *Leucocytes*.—The leucocytes of grouse are a subject of much intrinsic difficulty, and it is impossible to consider the grouping arrangement given below as more than provisional. The classification of the leucocytes of birds can be placed on a really sound basis only when detailed knowledge of the development of *all* the elements of the blood of birds has been obtained. In spite of good work by Denys, Dantschakoff, and others, such a complete developmental investigation of the blood of birds is still wanting. Owing both to the lack of time at my disposal and to the great scarcity of *quite fresh* material, I am unable to attempt such

an investigation, and therefore have availed myself of the classification at present adopted by such authorities as Burnett (1908), modifying their statements in accordance with my own personal observation and adding a number of details hitherto overlooked.

1. *Lymphocytes* (Pl. LXIII. figs. 5, 6).—The lymphocytes are the smallest of the leucocytes. They are from  $5.5\ \mu$  to  $8\ \mu$  in diameter approximately. They are smaller than the average red corpuscles. Each lymphocyte possesses a well-marked round or oval nucleus which is relatively large and occupies most of the cell. The cytoplasm of the lymphocyte is small in amount, is basophile, and is reduced to a rim around the nucleus. The lymphocytes have a great tendency to collect together in groups on blood-smears, and in such aggregations the cytoplasm of the members away from the periphery of the group is reduced to a minimum.

The lymphocytes are sometimes subdivided into large and small varieties. The larger specimens of lymphocytes gradually merge into the small mononuclears, and the naming and classifying of such leucocytes is often a matter of personal opinion.

2. *Large Mononuclear Leucocytes* (Hyaline cells).—These are large, approximately circular cells averaging  $9\ \mu$  to  $11.5\ \mu$  in diameter (Pl. LXIII. figs. 7, 8). In a film stained with Giemsa's fluid the mononuclear leucocytes are easily distinguishable not only from their large size but also from the fact that their cytoplasm stains a vivid blue and the nucleus a beautiful purple. The general cytoplasm of the cell is almost homogeneous in character.

The nucleus of a mononuclear leucocyte of grouse is large, occupying about half of the cell, and is often round or oval (figs. 5, 6). At other times the nucleus is somewhat curved or indented (fig. 8). The chromatin of the nucleus takes the form of a fairly dense mass, exhibiting in stained specimens a uniformly mottled appearance; it is situated to one side of the cell.

With Jenner's stain the nucleus colours a rather deep blue, while the cytoplasm stains only a faint blue and so is slightly basophile.

As Burnett (1908, p. 35) writes: "One can find all stages between typical lymphocytes with a small amount of strongly basophile, coarsely reticular cytoplasm and typical large mononuclears with a much larger amount of faintly basophile, finely reticular cytoplasm."

3. *Polymorphonuclear leucocytes* (Burnett) or *Crystalloid eosinophile cells* (Cullen, Warthin).—The apparently polymorphonuclear leucocytes of birds exhibit marked differences from those of mammals as regards the contained granules.

These cells in grouse are round, as seen in stained preparations, and measure from  $9\ \mu$  to  $9.5\ \mu$  in diameter (figs. 10-12). The

nucleus consists of two or more lobes and varies in shape—in other words, is polymorphous. The nucleus is fairly well stained with Jenner's stain and is coarsely reticular (figs. 10-12). The cytoplasm stains very faintly.

Embedded in the general cytoplasm are a number of bodies or granules which stain red with Jenner's stain and are oxyphilic. The bodies are generally described as spindle-shaped with tapering ends, but their outline has also been compared with that of a torpedo or cigar (fig. 11). Other leucocytes are found with thinner inclusions or "granules" which are rod-like in shape (fig. 10).

Cullen (1903) writes: "As to the nature and origin of these spindles [inclusions in the cytoplasm of the leucocytes] very little is known that is definite. They are certainly not artifacts, for they can be seen in fresh blood as well as in dried specimens. Dr. Simon is of the opinion that they may be derived from the second variety [the coarsely eosinophile leucocytes, mentioned next], in which granules take the place of spindles; that they are crystalloids and analogous to similar formations that have been encountered in certain tissues in man, and notably in the epithelial cells of the seminal tubules. He thinks that they result from the granules through loss of water, and as a matter of fact it is possible to reconvert the crystalloids into granules in the wet preparation by adding a droplet of a dilute solution of eosin from the side of the cover-glass. Dr. Simon has also noted that in certain preparations in which the eosinophilic material is present in one dense, apparently undifferentiated mass, the crystalloids separate out upon the application of heat."

In a few cases, the centre of the spindle bodies is occupied by a tiny circle or dot, which does not stain as deeply as the rest of the spindle and is refringent (fig. 12). The presence of this central dot is noticeable in the case of large spindles.

As regards the staining properties of the spindle bodies (crystalloids), I agree with Burnett that they are not intensely eosinophilic, but that "in affinity for stains the [spindle] granules resemble the polymorphs rather than the eosinophiles." Cullen, on the other hand, considers that the crystalloids are more oxyphilic than the true eosinophile leucocytes. Perhaps the differences of opinion of the various investigators are explicable by reference to slight variation in the stains used.

The distribution of the cytoplasmic inclusions within the cell is dependent on the shape and position of the nucleus.

4. *Eosinophile leucocytes* (Burnett) or *coarsely granular eosinophile (oxyphilic) cells*.—These cells are also present in the blood of normal grouse (figs. 13-15), but are more numerous in the blood of birds suffering from helminthiasis. The eosinophile cells are from  $8\ \mu$  to  $10\ \mu$  in diameter, and have a general resemblance to the polymorphonuclear leucocytes, only differing in the form of the inclusions or granules.

The shape of the eosinophile leucocyte is round (figs. 14, 15) or somewhat quadrilateral (fig. 13). The general cytoplasm is pale staining and slightly reticulate in structure. The nucleus usually resembles that of the polymorphonuclear leucocyte, and is mostly bilobed—the lobes being coarsely reticular and usually staining fairly deeply. The cell-body contains numbers of coarse, oxyphile (acidophile) granules which stain deeply with eosin. The granules are often rounded (figs. 13–15); they vary in size, some eosinophiles containing large granules (fig. 13) which may be relatively fewer in number, while in other cases the granules are small (fig. 14), and may be relatively more numerous. Eosinophiles with large granules are the more prevalent. The contour of the granules is generally round, but sometimes cells containing somewhat ovoid granules are seen which stain intensely with eosin.

Occasionally eosinophile cells are found in stained films the granules of which vary in shape within the same cell, some being round, some ovoid, and some almost spindle-shaped. Such cells and their contained granules may be somewhat deformed in the making of the film, otherwise it is difficult to classify these cells which are intermediate between crystalloid (polymorphonuclear) and granular eosinophiles.

Mononuclear eosinophile cells are occasionally seen in the blood of normal grouse, and perhaps represent an early stage of development of the polymorphonuclear eosinophiles. Such mononuclear cells are somewhat smaller than those depicted in Pl. LXIII. figs. 13–15, and have round nuclei. They are rare, and are perhaps analogous to the young eosinophile myelocytes of man.

5. *Mast cells* (coarsely granular basophile cells) are present in the blood of normal grouse (figs. 16, 17). They are rare. The cells are more or less rounded, with a pale staining cytoplasm. The nucleus is usually rounded (fig. 17) or slightly polymorphous (fig. 16), and stains blue with Jenner's stain—rather more deeply than similar cells in mammals.

Basophile granules, which vary in size and in number, occur in the cytoplasm. The granules are usually rounded and stain a deep purplish colour with Jenner's stain—in other words the granules are metachromatic. Mast cells measure from  $9\text{ }\mu$  to  $10\cdot5\text{ }\mu$  in diameter.

(c) *Thrombocytes* also occur in the blood of grouse (fig. 4). In the fresh condition they suggest very narrow and slightly small erythrocytes. They are often elliptical, with an oval nucleus centrally placed.

When stained the cell-body is pale and vacuolated, suggesting a coarsely reticular cytoplasm. The whole cell is basophile in its reactions, staining rather faintly blue with Jenner's stain.

Thrombocytes in grouse average  $9\text{ }\mu$  by  $4\text{ }\mu$ .

These elements may collect in clumps, and show a marked tendency to degeneration.

Red cells without nuclei were occasionally found in the blood of grouse. Such non-nucleate cells, however, were very rare.

At times there also appeared to be a number of free nuclei in the blood of grouse. In this connection we may note that Warthin (1907) found 16.5 per cent. of degenerated cells in the blood of normal fowls.

*Erythroblasts* occur in the blood of grouse in small numbers. The cells, which are nucleated, are rounder than erythrocytes, and are devoid of haemoglobin. The nucleus of an erythroblast is more spherical than that of an erythrocyte. The general cytoplasm is homogeneous, staining blue with Giemsa's stain.

The number of leucocytes found per cubic millimetre in the blood of apparently healthy grouse varied from 22,000 to 50,000, averaging about 32,000 per c.mm.

The average results of the differential counts of leucocytes of apparently healthy grouse may be tabulated thus:—

Lymphocytes .....	57 per cent.
Large mononuclears .....	19 " "
Polymorphonuclears (crystalloid eosinophiles) .	20 " "
Eosinophiles (coarsely granular eosinophiles)...	3 " "
Mast cells (basophiles) .....	1 " "

The difficult computations are those of the large mononuclears and lymphocytes. There are many medium sized mononuclears in grouse, which different observers would classify differently.

#### IV. PATHOLOGICAL BLOOD OF GROUSE.

The association of altered conditions of the blood with the presence of protozoal parasites has been noted already, and I have found certain alterations in the relative proportions of the blood cells of grouse that harboured Protozoa—Leucocytozoa, Spirochaetes and Coccidia—while other differences are to be associated with helminthiasis. The results may now be summarised:—

(a) When *Spirochaeta lagopodis* [Fantham (1910)] was present in the blood of grouse, as it was to some extent in two specimens, the number of mononuclear leucocytes increased and these leucocytes became slightly enlarged and vacuolated (Pl. LXIII. fig. 9). Levaditi (1901) noticed the presence of vacuolated mononuclear leucocytes in the blood of fowls infected with *Spirochaeta gallinarum*, together with mononuclear and polynuclear leucocytosis. Balfour (1908) found vacuolated mononuclear leucocytes in the blood of fowls suffering from spirochaetosis in the Soudan. The infection of grouse with *S. lagopodis* was probably not nearly as

great as that of fowls with *S. gallinarum* investigated by Levaditi and Balfour.

( $\beta$ ) The presence of *Leucocytozoon lovati* in the blood of grouse is associated with mononuclear leucocytosis. A differential leucocyte count of the blood of one of the grouse containing *L. lovati* gave:

Lymphocytes .....	63.0	per cent.
Large mononuclears .....	28.0	" "
Polymorphonuclears .....	5.5	" "
Eosinophiles .....	2.5	" "
Mast cells .....	1.0	" "

There was also evidence of polychromatophilia in the red cells of grouse infected with *Leucocytozoon lovati*.

( $\gamma$ ) *Eimeria (Coccidium) avium* also has its effect, indirectly, on the blood. Birds suffering from coccidiosis became anæmic. The paleness of the blood is due to the diminished number of red cells in the blood. Estimations of the hæmoglobin value by Tallqvist's scale gave 60-70 in the case of grouse chicks suffering from coccidiosis, 80-90 for healthy grouse chicks.

There is an increased number of polymorphonuclear leucocytes (crystalloid eosinophiles). Differential leucocyte counts of two grouse-chicks dying from coccidiosis gave:

Polymorphonuclears .....	31.5 to 39.5	per cent.
Eosinophiles .....	3.5 to 5.5	" "
Large mononuclears .....	13.0 to 31.0	" "
Lymphocytes .....	26.0 to 50.0	" "
Mast cells .....	0.6	per cent.

In Mammals an increase in the number of polymorphonuclear leucocytes occurs in inflammation, especially locally. The increase in polymorphonuclear leucocytes (crystalloid eosinophiles) is probably to be associated with the intestinal inflammation caused by the presence of Coccidian parasites.

Similarly in a fowl chick dying of coccidiosis, I obtained the following differential leucocyte count:

Polymorphonuclears .....	47	per cent.
Eosinophiles .....	2	" "
Mononuclears .....	29.5	" "
Lymphocytes .....	20.5	" "
Mast cells .....	1	" "

The blood of this fowl chick\* contained basophile spindle-shaped cells (Pl. LXIII. fig. 18).

( $\delta$ ) *Helminthiasis* is common in grouse. The various worms found in grouse have been well described by Shipley (1909).

\* Burnett gives the following differential leucocyte count of normal fowl's blood:—Polymorphonuclears 28.8 per cent., eosinophiles 3.3 p. c., large mononuclears 5.5 p. c., lymphocytes 58 p. c., mast cells 4.3 p. c.

Grouse which would be considered perfectly healthy by keepers have often contained a few worms. The causal factor of disease in adult grouse is the larval stage of *Trichostrongylus pergracilis*, as shown by the researches of Dr. Leiper (Abstr. Proc. Zool. Soc. Lond. No. 80, March 1, 1910). The adult *Trichostrongylus* occurs in the caeca of grouse, and sets up inflammation therein. In the blood of three adult birds dying on the moors from grouse disease, I obtained differential leucocyte counts which may be thus summarised :

Eosinophiles .....	23·5 to 42·0 per cent.
Polymorphonuclears .....	7·5 to 14·0 " "
Mononuclears .....	6·0 to 10·0 " "
Lymphocytes .....	44·0 to 62·5 " "
Mast cells .....	0·5 per cent.

Contrasting these counts with those given for normal grouse, the occurrence of eosinophilia is deduced. All three of these birds, dying of "grouse disease," had many *Hymenolepis microps* in their duodenum in addition to *Trichostrongylus* in the caeca.

Eosinophilia is often associated with helminthiasis in mammals. Helminthiasis in grouse results not only in an increase in the number of eosinophile leucocytes, but also in a diminution of the number of erythrocytes in the diseased birds. Thus the number of red cells found in an adult cock grouse dying from helminthiasis was 3,250,000 per cubic millimetre—the number of red cells for a normal cock grouse being about one million more. The hæmoglobin value estimated by Tallqvist's scale was 60 for a grouse suffering from helminthiasis and 80–90 for healthy adult grouse.

In spite of the incomplete character of this investigation of the blood of the grouse (due to the lack both of material and time at my disposal), I think that there are sufficient results contained herein to emphasise the importance of parallel investigations of the blood in connection with all animal diseases.

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*Proc. Zool. Soc. Lond.* 1909, pp. 335-350, 8 pls.
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## EXPLANATION OF PLATE LXIII.

All figures were outlined with Abb -Zeiss camera lucida, using Zeiss 2 mm. apochromatic immersion objective and compensating ocular 12. Preparations stained with Jenner's stain.

The magnification is in all cases approximately 2000 diameters.

- Fig. 1. Erythrocyte of Grouse.  
 2. Erythrocyte of Pigeon.  
 3. Erythrocyte of Fowl.  
 4. Thrombocyte of Grouse.  
 5, 6. Lymphocytes of Grouse.  
 7, 8. Mononuclears of Grouse.  
 9. Mononuclear leucocyte of Grouse showing vacuolations internally. From a bird suffering from slight spirochaetosis.  
 10-12. Polymorphonuclears (Burnett) or crystalloid eosinophile cells (Cullen) of Grouse. In fig. 10 the cytoplasmic enclosures are rod-like, in fig. 11 they are spindle-shaped bodies, while in fig. 12 the spindle bodies have small clear central areas.  
 13-15. Eosinophile leucocytes of Grouse (coarsely granular eosinophiles of Cullen). The figures represent the variation in the size and shape of the eosinophile granules. Figs. 13, 15 represent the commonest forms of eosinophiles.  
 16, 17. Mast cells (basophiles) of Grouse, showing metachromatic basophile granules in cytoplasm.  
 18. Elongate tailed cell occurring in the blood of a Fowl chick. The chick was suffering from coccidiosis. Some authors consider such spindle-shaped or tailed cells to be normal to the blood of birds and reptiles. Extremely few such cells occur in the blood of normal Grouse.



5. Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunningham, F.Z.S., 1904-1905.—Report on the Ostracoda. By Prof. G. O. SARS, C.M.Z.S.

[Received February 21, 1910.]

(Plates LXIV. LXXIII.)\*

*Introduction.*

In a paper published in the Society's 'Proceedings' (1909, p. 31), I have given an account of the Copepoda found in the samples taken by Dr. Cunningham, during the Third Tanganyika Expedition, from the three large Central African lakes, and I mentioned in this paper that a number of Ostracoda also occurred in the samples, some of the species having already been observed by Dr. Cunningham, and separated by him in small tubes. I have now examined the material more closely, and give in the present paper an account of the species accompanied by carefully drawn figures of all of them. The number of species determined amounts to no less than 29 in all, belonging to 7 different genera. Only two of these species I have been enabled to identify with previously described forms; all the others seem to be new to science. In the following pages I give short descriptions of all the species, with remarks on affinity and occurrence, and at the close of the paper some general remarks are added.

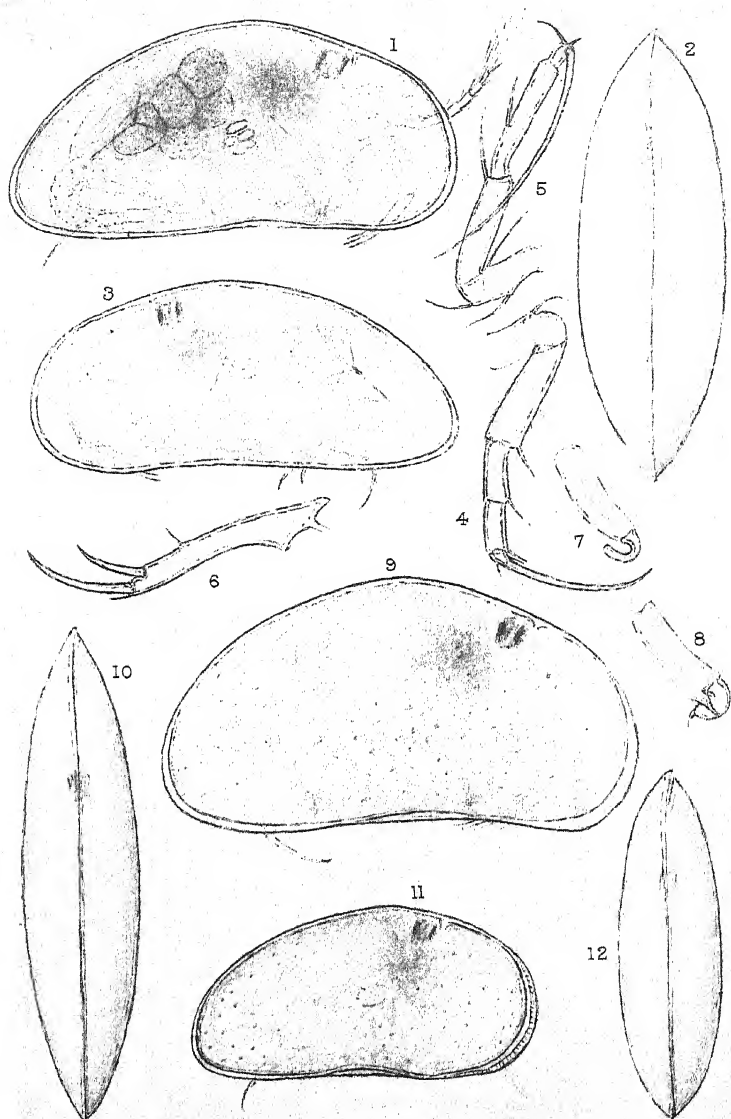
*Description of the Species.*

Family CYPRIDÆ.

Genus 1. PARACYPRIDÆ, gen. n.

*Generic Characters.*—Shell compressed, of various form in the different species, in some cases approaching that in *Cypria*, in other cases very different, being, as a rule, very thin and pellucid, so as to allow the enclosed animal to be rather distinctly traced through its walls. Valves more or less unequal, the right one being the smaller and in some cases conspicuously overlapped by the left both in front and behind. Surface of shell more generally smooth and only very sparingly hairy at each extremity. Limbs on the whole built upon the same type as in *Cypria* (see the detail-figures given on Pl. LXV. of one of the species). Caudal rami comparatively short and more or less curved, tapering distally, dorsal edge smooth; terminal claws of moderate size; dorsal seta generally well developed, apical seta very small. Inferior antennæ of male with the third joint distinctly subdivided. Copulatory appendages each terminating in a beak-like extremity consisting of two jaws, one of which is mobile.

\* For explanation of the Plates see p. 757.



G.O. Sars

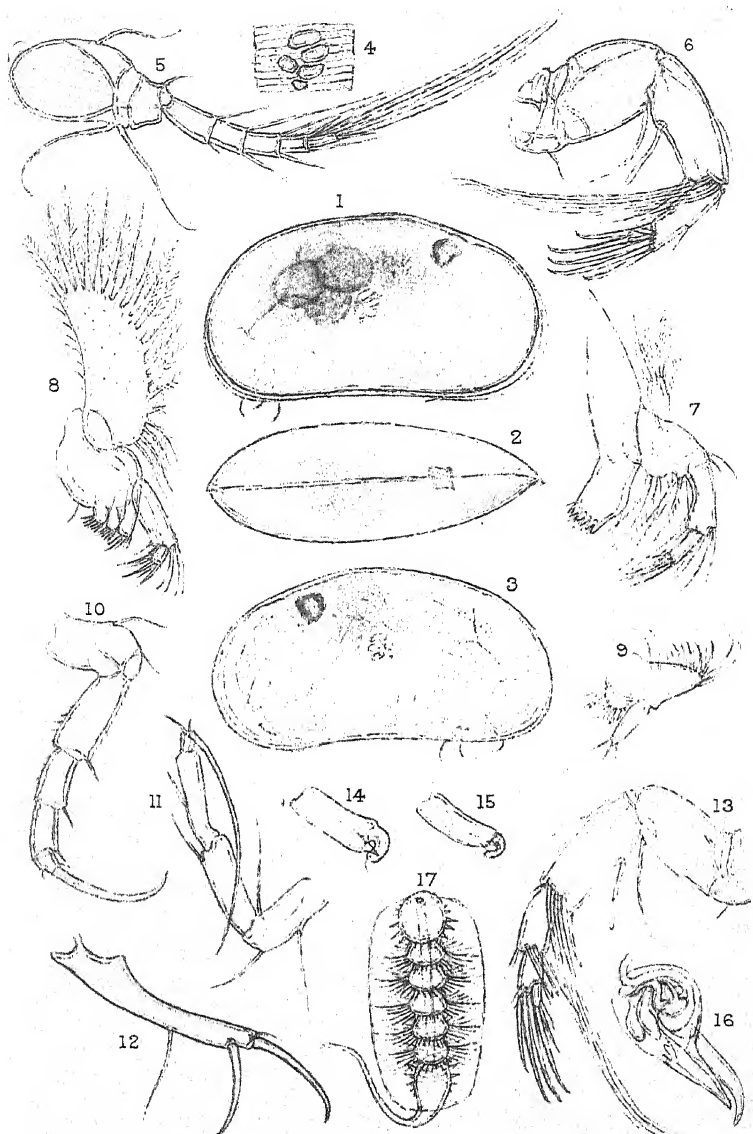
London Stereoscopic Co. imp

1-8. *PARACYPRID DECLIVIS* G.O.SARS.

9-10. *P. COMPLANATA* G.O.SARS.

11-12. *P. CONOIDEA* G.O.SARS.



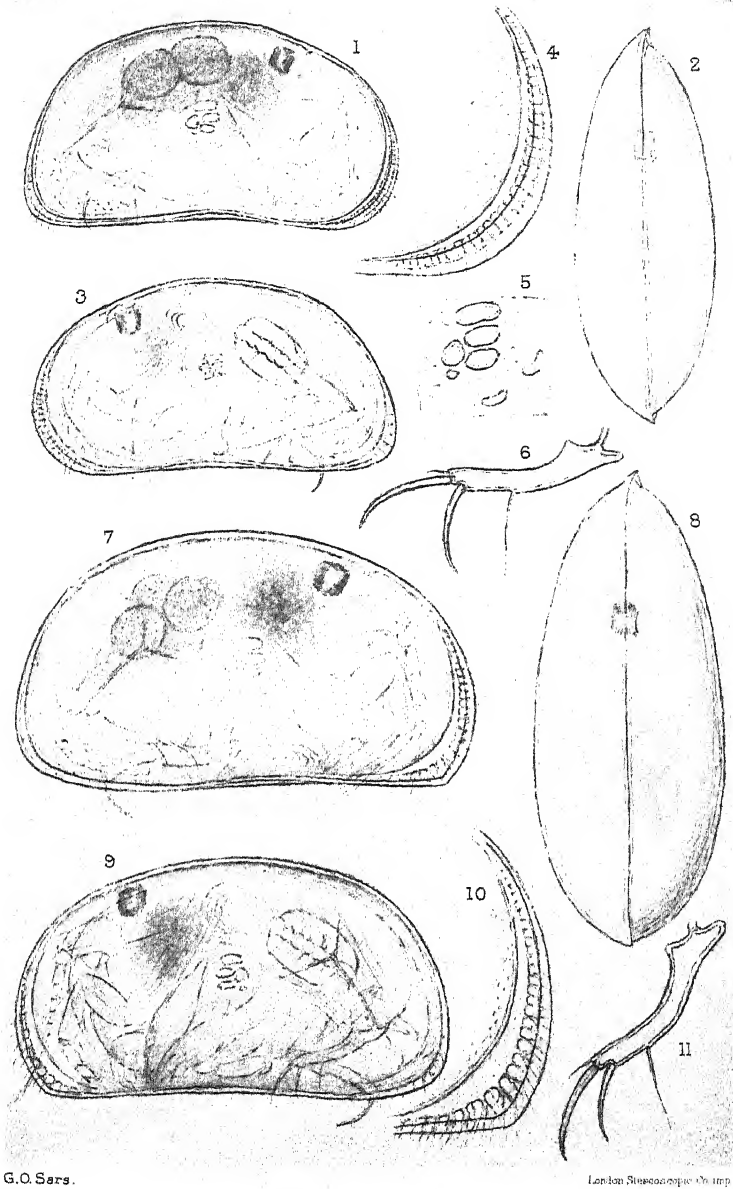


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London Stereoscopic Co. Ltd.

PARACYPRIA OBTUSA G.O.SARS.





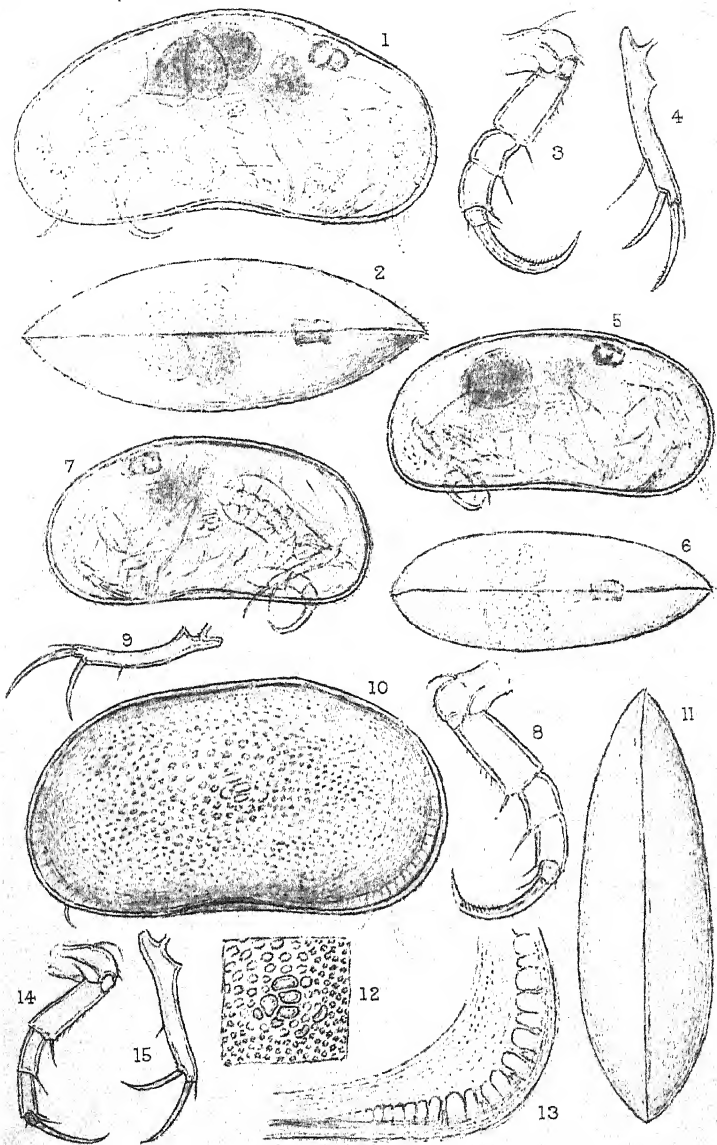
G.O. Sars.

London Stereoscopic Co. imp.

1-6. *PARACYPRIA DEFLEXA* G.O.SARS.

7-11. *P. SUBANGULATA* G.O.SARS.





G.O. Sars.

London Stereoscopic Co. imp.

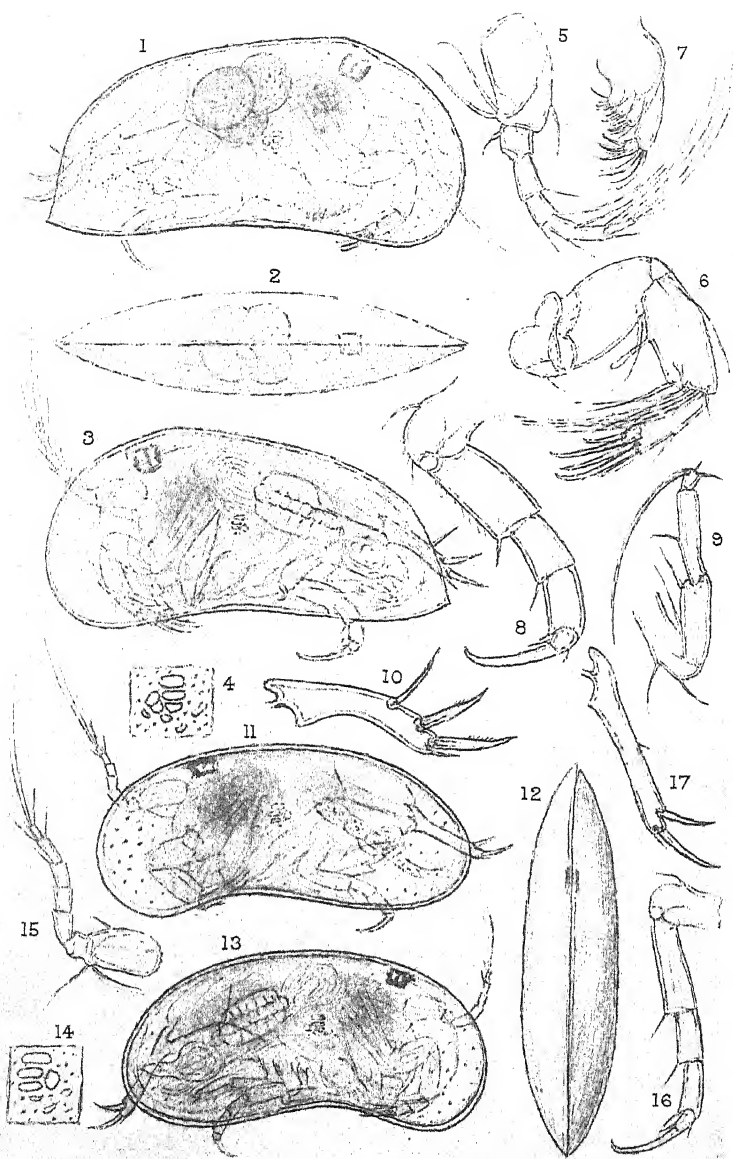
1-4. *PARACYPRID RENIFORMIS* G.O.SARS.

5-9. *P. HUMILIS* G.O.SARS.

10-15. *P. OPACA* G.O.SARS.







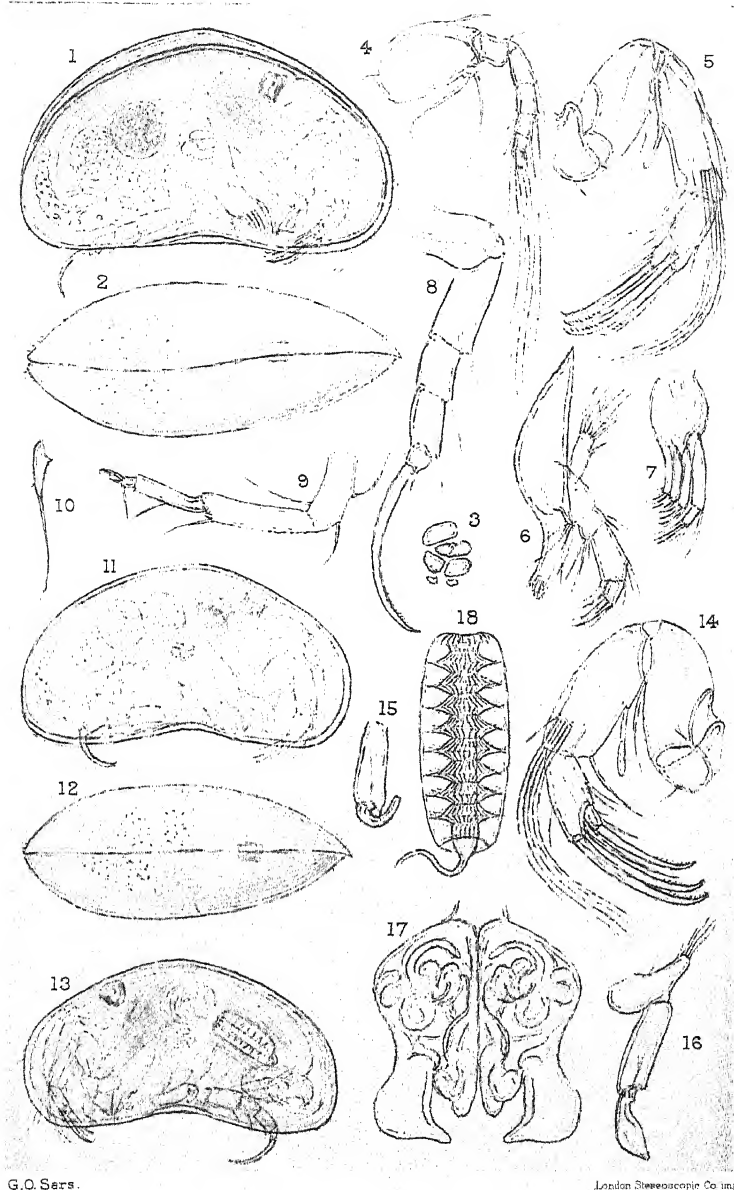
G. O. Sars.

London Stereoscopic Co. imp.

1-10. *PARACYPRIA CLAVIFORMIS* G.O.SARS.

11-17. *P. FLEXUOSA* G.O.SARS.





G.O. Sars.

London Stereoscopic Co. imp.

1-10. CYPRIDOPSIS OBLIQUATA G.O.SARS.

11-18. C. SINUATA G.O.SARS.





G.O. Sars.

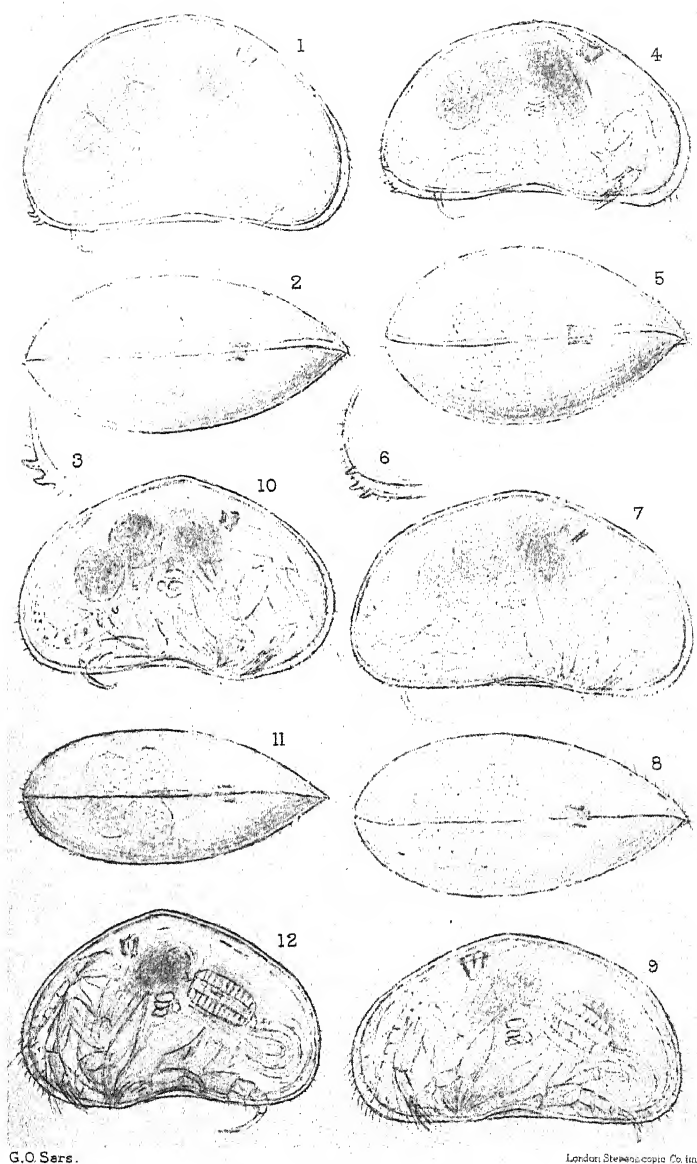
London Stereoscopic Co. Imp.

1-3. CYPRIDOPSIS CUNNINGTONI G.O.SARS.

4-6. C. PUSILLA G.O.SARS. 7-9. C. MONODONTA G.O.SARS.

10-12. C. SERRATA G.O.SARS





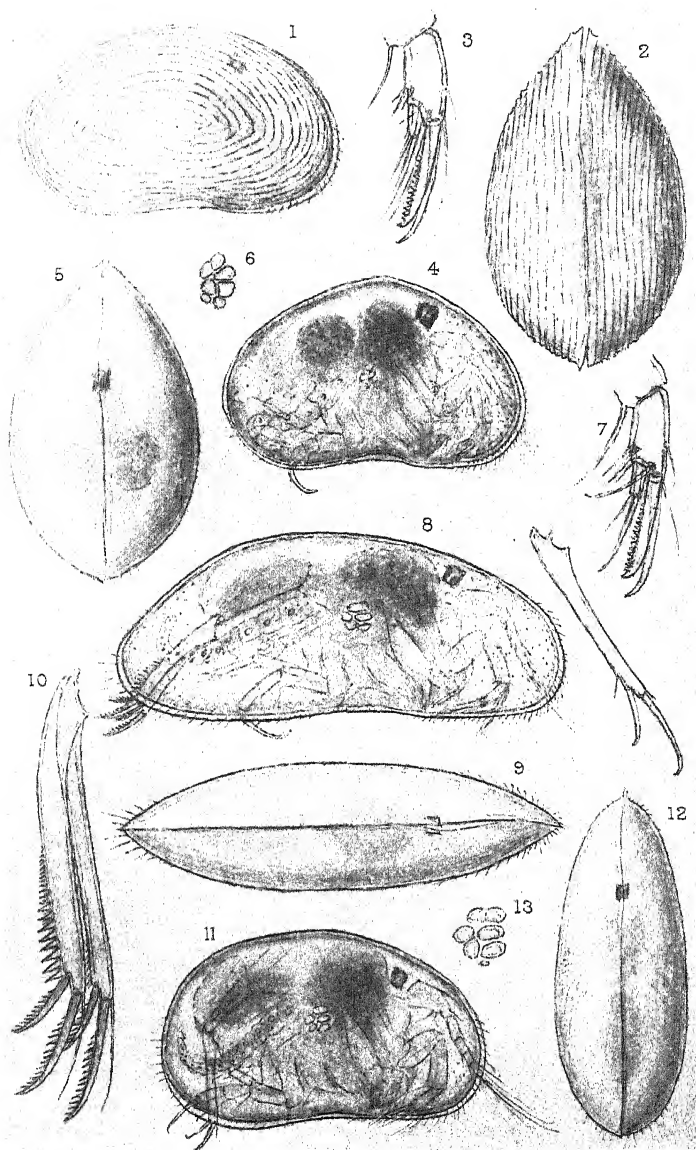
1-3. CYPRIDOPSIS BIDENTATA G.O.SARS.

4-6. C. TUMIDULA G.O.SARS.

7-9. C. CONGENERA G.O.SARS. 10-12. C. GIBBA G.O.SARS.







G.O. Sars.

London Stereoscopic Co. imp.

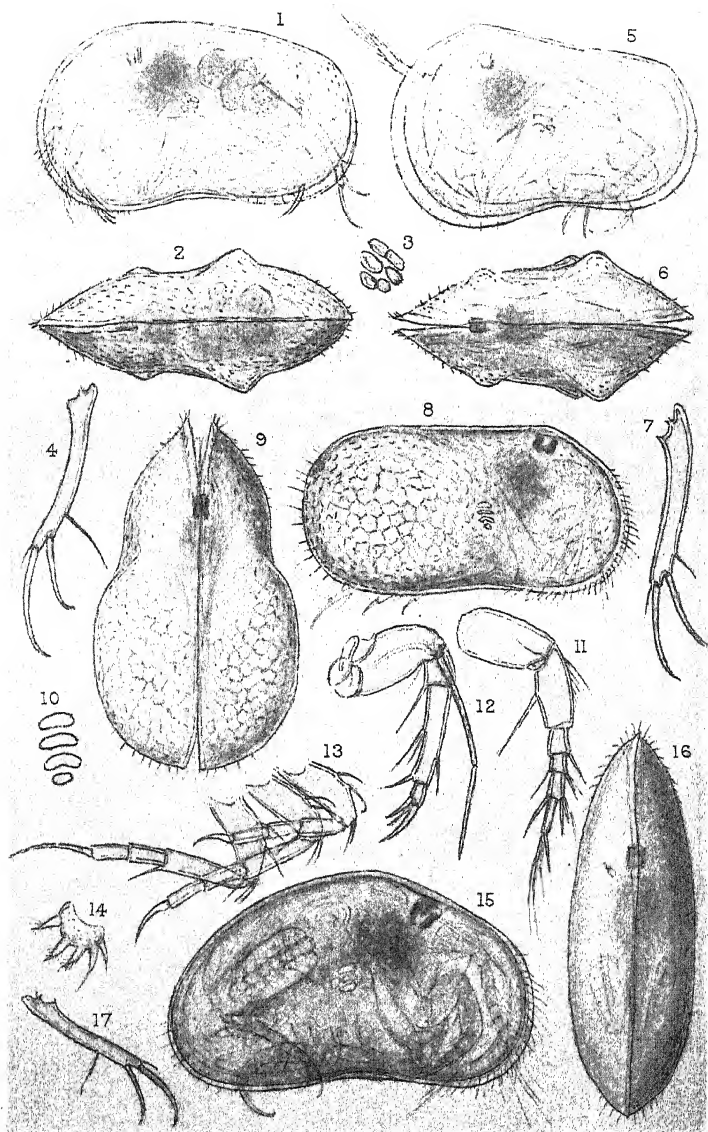
1-3. ZONOCYPRIS COSTATA VÄVRA.

4-7. Z. LÆVIS G.O.SARS.

8-10. STENOCYPRIS PERARMATA BRADY.

11-14. HETEROCYPRIS DUBIA G.O.SARS.





G.O. Sars.

London Stereoscopic Co. Imp.

1-4. *ILYOCYPRIS PROPINQUA* G.O.SARS.

5-7. *I. ALTA* G.O.SARS.

8-14. *LIMNICYTHERE OBTUSATA* G.O.SARS.

15-17. *PARACYPRIA CURTA* G.O.SARS.



Ejaculatory tubes each with eight whorls of chitinous stripes, both extremities conspicuously dilated and encircled by a row of coarser spiniform processes.

*Remarks.*—The type of this new genus is the form described by the present author from a brackish-water lagoon on the Chatham Islands under the name *Paracypris tenuis*\*. It was, indeed, only with great doubt that I provisionally referred this form to the marine genus *Paracypris* G. O. Sars. I now find that it is much more closely related to the genus *Cypria* Zencker, for which reason I propose to name the new genus *Paracypria*. The species from the Chatham Islands is closely allied to some of the Tanganyika species, as will be shown below. No less than twelve different species referable to this genus have been found in the samples.

1. *PARACYPRIA DECLIVIS*, sp. n. (Plate LXIV. figs. 1-8.)

*Specific Characters.*—**FEMALE.** Shell moderately compressed; seen laterally (fig. 1) of oblong cuneiform shape, greatest height occurring somewhat in front of the middle and not attaining half the length, anterior extremity obtusely rounded, posterior much narrower and ending below in a somewhat conical blunt corner, dorsal margin strongly curved in the middle and sloping evenly behind to the posterior corner, ventral margin nearly perfectly straight; seen dorsally (fig. 2) narrow oblong in form, with the greatest width about equalling one-third of the length, both extremities acuminate, side-edges nearly parallel in the middle. Valves only slightly unequal and very thin and pellucid, with very slight trace of hairs at the extremities. Surface of shell quite smooth and shining, without any distinct sculpturing. Limbs (figs. 4, 5), on the whole, very like those in the type species; the slender dactylus of the anterior legs (fig. 4), however, quite smooth, without any trace of lateral denticles. Caudal rami (fig. 6) slightly curved at the base; claws rather strong and perfectly smooth, the distal one much the larger and exceeding half the length of the ramus; dorsal seta small, but distinct.

**MALE** (fig. 3) a little smaller than female, and having the shell somewhat less vaulted dorsally. Prehensile palps of posterior maxillæ (figs. 7, 8), as usual, somewhat unequal on left and right sides, and apparently differing a little in shape from those in the type species.

Length of shell ♀ 0.91 mm., height 0.42 mm., width 0.30 mm.

*Remarks.*—This form is closely allied to the type species, exhibiting a very similar shape of the shell. It is, however, of considerably larger size, and moreover differs in the less compressed shell and in the more robust and quite smooth caudal claws. Nor is there any trace of the fine denticles found in *P. tenuis* on the dactylus of the anterior legs.

\* Zool. Jahrbücher, vol. xxi. pt. 4, p. 404, pl. xx. figs. 173-186.

*Occurrence.*—Solitary specimens of this fine species were found in three different samples from Tanganyika. One of these samples (88) was taken 7/9/04 at Niamkolo (S. end of lake), another (97) 19/9/04 at about the same place, and the third (138) 13/10/04 at Sumbu (S.W. of lake).

2. *PARACYPRIA COMPLANATA*, sp. n. (Plate LXIV. figs. 9, 10.)

*Specific Characters.*—MALE. Shell highly compressed; seen laterally (fig. 9) oval reniform in shape, greatest height occurring about in the middle and equalling half the length, anterior extremity obliquely rounded and somewhat deflexed, posterior narrower and obtuse at the end, dorsal margin almost angularly curved in the middle and sloping behind with a slight curve to the posterior extremity, ventral margin slightly concave in the middle; seen dorsally (fig. 10) very narrow, with the greatest width scarcely exceeding one-quarter of the length. Valves rather pellucid and somewhat more unequal than in the preceding species, the right one being conspicuously overlapped by the left at the anterior extremity below. Surface of shell with scattered dots and finely hairy at both extremities.

Length of shell 0.96 mm., height 0.49 mm., width 0.24 mm.

*Remarks.*—This form is of still larger size than the preceding one, from which it moreover differs conspicuously in the form and sculpture of the shell. The structure of the several appendages could not be sufficiently examined in the solitary specimen found, but no essential difference in this respect from that in the preceding species was to be traced.

*Occurrence.*—Only a single specimen of this form, a fully grown male, has been secured. It was found in a sample from Tanganyika (242) taken 1/3/05 at Kaboge (N.W. shore of the lake).

3. *PARACYPRIA CONOIDEA*, sp. n. (Plate LXIV. figs. 11, 12.)

*Specific Characters.*—MALE. Shell rather compressed; seen laterally (fig. 11) of a narrow, somewhat conoid shape, greatest height occurring far in front and about equalling half the length, anterior extremity evenly rounded and much broader than the posterior, which is conically tapered, though obtuse at the end, dorsal margin gently curved and sloping evenly behind to the posterior corner, ventral margin nearly straight; seen dorsally (fig. 12) narrow oblong in form, with the greatest width about equalling one-third of the length, both extremities obtusely acuminate. Valves moderately pellucid and rather unequal, the right being considerably overlapped by the left along the whole anterior extremity; lip of the latter somewhat thickened and giving origin to a row of very delicate hairs. Surface of shell dotted in a similar manner to that in *P. complanata*.

Length of shell 0.49 mm., height 0.24 mm., width 0.15 mm.

*Remarks.*—This is a rather small species, being scarcely more

than half as large as *P. complanata*. The specimen examined is, however, evidently fully grown, as proved by the well-developed ejaculatory tubes shining through the pellucid shell. The shape of the latter conspicuously differs from that of either of the two preceding species.

*Occurrence*.—A solitary male specimen of this form was found in a sample from Tanganyika (138), taken 13/10/04 at Sumbu (S.W. of lake).

#### 4. PARACYPRIA OBTUSA, sp. n. (Plate LXV.)

*Specific Characters*.—FEMALE. Shell moderately compressed; seen laterally (fig. 1) of oval or elliptical shape, greatest height occurring about in the middle and slightly exceeding half the length, both extremities obtusely rounded and nearly equal, dorsal margin gently curved with trace of an angle behind the ocular region, ventral margin very slightly concaved in the middle; seen dorsally (fig. 2) oblong in shape, greatest width somewhat exceeding one-third of the length and occurring a little behind the middle, anterior extremity narrower and more acuminate than the posterior. Valves rather thin and pellucid, conspicuously unequal, the right one being overlapped by the left along the whole anterior extremity, as also a little behind; anterior lips of both valves bordered by a very thin and pellucid rim. Surface of shell exhibiting a very fine longitudinal striation, only visible under high magnifying-powers (fig. 4), and clothed at each extremity with extremely delicate hairs. Inner coating of valves exhibiting a somewhat irregular reticulation, more conspicuous at the anterior extremity (fig. 1). Limbs (figs. 5-11) on the whole somewhat more strongly built than in the type species, but otherwise identical in structure. Caudal rami (fig. 12) slightly curved, with the claws moderately strong and less unequal than in *P. declivis*, the distal one about equalling half the length of the ramus; dorsal seta well developed and rather slender.

MALE (fig. 3) of about same size as female, and having the shell very similar in shape. Sexual characters, manifested in the structure of the inferior antenna (fig. 13), the palps of the posterior maxillæ (figs. 14, 15), the copulatory appendages (fig. 16), and the ejaculatory tubes (fig. 17), agreeing exactly with those in other species of this genus.

Length of shell 0.63 mm., height 0.33 mm., width 0.22 mm.

*Remarks*.—In the general shape and sculpture of the shell, this form exhibits a certain resemblance to the species of the genus *Cypria* Zencker, and, indeed, at first I was inclined to regard it as a member of that genus. On a closer comparison and examination of the several appendages, I find it, however, impossible to separate this form generically from the other species here recorded as belonging to the genus *Paracypria*.

*Occurrence*.—This species seems to be by far the commonest of the Ostracoda of the Tanganyika Expedition. I have noted it



in five of the samples from Tanganyika, and in some of these it occurred rather abundantly. The localities are as follows: No. 82, Kituta Bay (S. end of lake), No. 97, Niamkolo (S. end of lake), No. 138, Sumbu (S.W. of lake), No. 169, Kala (E. shore of lake), No. 240, Buraka (N.W. shore). In the last-named locality it seems to have occurred in great abundance, and a good many of the specimens captured had also been separated from the sample by Dr. Cunningham and placed in a small tube.

5. *PARACYPRIA DEFLEXA*, sp. n. (Plate LXVI. figs. 1-6.)

*Specific Characters*.—FEMALE. Shell moderately compressed; seen laterally (fig. 1) of oval reniform shape, greatest height occurring somewhat behind the middle and slightly exceeding half the length, anterior extremity evenly rounded, posterior scarcely narrower and obliquely deflexed, terminating in an obtusely triangular corner, dorsal margin evenly curved with the greatest curvature behind the middle and sloping rather steeply to the deflexed hind corner of the shell, ventral margin very slightly concave in the middle; seen dorsally (fig. 2) oblong-ovate in form, with the greatest width exceeding one-third of the length, anterior extremity somewhat narrower than posterior. Valves rather unequal, the right being considerably overlapped by the left both in front and behind, anterior lip of left valve (fig. 4) exhibiting a somewhat thickened zone crossed by numerous grooves, from the bottom of which delicate hairs arise. Surface of shell smooth and shining, though exhibiting a few small dots similar to those found in *P. complanata* and *P. conoidea*. Muscular impressions in the centre of each valve (fig. 5) very distinct and arranged as in the other species of this genus. Caudal rami (fig. 6) distinctly curved; claws moderately strong and only slightly unequal, the distal one exceeding half the length of the ramus; dorsal seta well developed and rather slender.

MALE (fig. 3) a little smaller than female, but exhibiting a closely similar shape of the shell.

Length of shell ♀ 0.75 mm., height 0.40 mm., width 0.26 mm.

*Remarks*.—In external appearance this form somewhat resembles a *Candona*, the shell exhibiting in the lateral aspect a rather similar shape and having the hind corner deflexed in a similar manner to that found in the more typical species of that genus. It is, however, a true *Paracypria*, as proved by the examination of the several appendages, which agree closely in structure with those in *P. obtusa*.

*Occurrence*.—Of this species also a considerable number of specimens has been secured. I have noted it in four of the Tanganyika samples. In two of these samples (138 and 240) it occurred rather plentifully in company with *P. obtusa*. In the other two (97 and 169) only solitary specimens were found. The localities from which the samples were taken have been recorded above.

no large ducts comparable with those we have seen in the glands consisting of folded epithelium; on the contrary, the only ducts visible are narrow slit-like channels occasionally to be detected in their course between the cells. These narrow channels vary in width greatly according to the state of activity of the gland; they are necessarily numerous (though by no means always to be observed) in order to provide means of exit to the surface for all the numerous cells concerned, and they open on the gland surface inside the bladder lumen by small pores. Also penetrating the mass of the gland are numerous fine capillaries supplying the individual cells with nutriment and oxygen on the sides remote from those facing the ducts just mentioned. All the intracellular structures previously mentioned as occurring in connection with cells of the gas gland are here shown in a very obvious manner. Figure 50 (Pl. VI.) shows intracellular lumina, one in longitudinal section. As to the significance of these intracellular passages found in gas gland cells, it is not necessary to regard them all as possessing purely a nutritive utility as Nusbaum & Reis have supposed; it seems more probable, judging from their appearance in such cases as that illustrated in figure 50, that some at least are concerned with the passage of the gas bubble from the interior of the cell to the exterior; they are very rare in their occurrence in my preparations and in transverse section closely resemble bubbles, especially if near the nucleus. The whole mass of cells composing the gas gland is therefore penetrated by capillaries and gland lumina. I have not observed a pancreas in the region of the rete in *Ophidium*.

*Other Examples of the Third or Ophidium Type of "Red Body."*

*Box boops* L.

The "red body" of *Box boops* has the curious macroscopic appearance shown in figure 51 (Pl. VI.). Figure 52 (Pl. VII.) is a diagram of a transverse section through the middle of the "red body," and the appearance of two concentric loops is thus seen to be due to the disposition of the rete mirabile. The primary artery and vein enter the "red body" posteriorly and break up into smaller arteries and veins (intertwined with pancreatic acini) to form the rete mirabile as usual. The glandular epithelium consists, as in *Ophidium*, of a mass of cells interpenetrated by capillaries and lumina, but here the cells are all approximately equal in size and the gas gland is more than a dozen cells thick.

*ATHERINA HEPSETUS* L.

In macroscopic appearance the "red body" of *Atherina hepsetus* is diffuse in form (Pl. VI. fig. 53) and consists of tufts of retia mirabilia borne laterally on a median pair of vessels (artery and vein) with corresponding tracts of glandular epithelium. The glandular epithelium (Pl. VII. fig. 54) is very similar to that of *Box boops*; in other words, it consists in its thickest parts of a mass of small cells, seven or eight cells in thickness, with inter- and

occasional intra-cellular ducts and capillaries. I have not observed a pancreas in the region of the rete. The cell-outlines of the gas gland are faint and a small amount of granular material is present in the bladder lumen in my preparation.

I stated above that the massive type of gas gland is quite distinct from the folded type in certain genera, and, indeed, these two types of bladder epithelium are almost always easily distinguishable from each other in the genera which I have studied: genera, with a few exceptions to be mentioned, either possess the folded or the massive type of gland and not glands intermediate in structure. In young specimens of *Atherina* about 15 mm. in length, that portion of the bladder epithelium which is about to produce the gas gland is at first composed of a single layer of cubical or short columnar cells, and it is worthy of notice that these cells, in order to build up the fully-formed massive gland, all divide at right angles to the plane of the bladder wall (Pl. VII. fig. 55), *i. e.* the successive planes of cell-cleavage are parallel with the plane of the bladder wall—the initial unilaminar epithelium never becoming folded at any stage of development. As the gas gland cells multiply connective tissue cells may be observed to extend in between them in order to furnish the connective and vascular tissues which penetrate the mass of the gland when fully formed. Also if figures 54 and 55 be compared, it will be seen that the cells (especially the nuclei) of the gas gland of the adult *Atherina* are noticeably smaller as compared with those in the young fish. The fact that there is no indication of folding of the bladder epithelium during development of the massive type of gland is important, since Reis (64) supposes, on the ground that there exist forms of bladder epithelium more or less intermediate in structure between the folded and massive types, that the latter has been derived from the former, and if such be the case we might expect that the massive type of gland in its development would pass through a folded developmental stage. As we have seen, this is not the case in *Atherina* and presumably not in other genera possessing typically massive glands. I assume this with the more confidence since in some gas glands which, owing to the exceedingly close apposition of the folds, at first sight appear to be massive, it is always possible to refer them at once to the folded type by observing in each such case the margins of the gland where it merges into the squamous epithelium lining the greater part of the bladder cavity, since here the folds are quite simple: such marginal folds are never present in true massive glands.

Reis, in contending that the massive type of gland is but a derivative of the folded type, instances as transitional forms between the two types the gas gland epithelia of *Syngnathus* and *Girardinus*. I have not examined *Girardinus*, but the gas gland epithelium of my specimens of *Syngnathus* can certainly not be said to be transitional, since, as my description above of this epithelium clearly shows, the massiveness of the gland merely results from the extreme length of the folds and their occasional anastomosis:

6. *PARACYPRIA SUBANGULATA*, sp. n. (Plate LXVI. figs. 7-11.)

*Specific Characters.*—FEMALE. Shell somewhat less compressed than in the preceding species; seen laterally (fig. 7) broadly oval in form, greatest height occurring nearly in the middle and considerably exceeding half the length, anterior extremity obliquely rounded and subangular below, posterior scarcely narrower and terminating in a slightly deflexed obtuse corner, dorsal margin forming a rather even curve, ventral almost straight; seen dorsally (fig. 8) oblong-oval in shape, greatest width occurring behind the middle and almost attaining half the length, both extremities somewhat blunted at the end. Valves less pellucid than in the preceding species and very unequal, the right one being considerably overlapped by the left both in front and behind; anterior lip of right valve simple and evenly curved, that of left valve (fig. 10) forming below an abrupt angular bend and exhibiting inside the hyaline border a thickened zone crossed by a number of somewhat irregular branching grooves. Surface of shell smooth and very finely hairy at each extremity. Caudal rami (fig. 11) considerably curved; claws of moderate size and slightly unequal, the distal one about half the length of the ramus; dorsal seta slender and elongated. Ends of ovarian tubes in this and the two preceding species deflexed.

MALE (fig. 9) a little smaller than female and having the shell somewhat less vaulted above.

Length of shell ♀ 0.86 mm., height 0.48 mm., width 0.39 mm.

*Remarks.*—This form is undoubtedly nearly related to the two preceding species, but is of considerably larger size than either of them, and is, moreover, easily recognized by the more vaulted shell and especially by the peculiar angular appearance of the anterior extremity caused by the projecting lip of the left valve.

*Occurrence.*—Only three specimens of this form, two females and one male, have come under my notice. They were found in a sample from Tanganyika (53) taken 9/8/04 at Niamkolo (S. end of lake).

7. *PARACYPRIA RENIFORMIS*, sp. n. (Plate LXVII. figs. 1-4.)

*Specific Characters.*—FEMALE. Shell not much compressed; seen laterally (fig. 1) oblong reniform in shape, greatest height occurring in the middle and not nearly attaining half the length, anterior extremity evenly rounded, posterior somewhat narrower and obtuse at the end, not deflexed, dorsal margin forming a quite even curve throughout, ventral one rather deeply sinuated in the middle; seen dorsally (fig. 2) oblong fusiform in shape, greatest width exceeding one-third of the length and occurring in the middle, both extremities acuminate. Valves very thin and pellucid, only slightly unequal; left valve, however, as usual, overlapping the right a little along the anterior extremity; lips

of both valves thin and pellucid. Surface of shell quite smooth, without any trace of sculpture, but distinctly hairy at both extremities. Eye very large and conspicuous. Anterior legs (fig. 3) much more coarsely built than in any of the preceding species, dactylus very strong, with falciform curve and clothed inside in its outer part with fine spinules. Caudal rami (fig. 4) of the structure characteristic of the genus, being slightly curved at the base and a little tapered distally; claws rather strong and finely spinulose inside, the distal one about half the length of the ramus; dorsal seta well developed. Ends of ovarian tubes not deflexed, but extending upwards along the posterior edges of the valves (fig. 1).

Length of shell 0.61 mm., height 0.28 mm., width 0.21 mm.

*Remarks.*—This form is easily distinguishable from any of the preceding ones by the narrow and pronouncedly reniform shell and by the coarsely built anterior legs. In the structure of the other limbs I have failed to detect any essential difference from those in the preceding species.

*Occurrence.*—Only two female specimens of this form have come under my notice. They were found in a sample from Tanganyika (169), taken 18/11/04 at Kala (E. shore of lake).

#### 8. PARACYPRIA HUMILIS, sp. n. (Plate LXVII. figs. 5-9.)

*Specific Characters.*—FEMALE. Shell rather compressed; seen laterally (fig. 5) of narrow elliptical form, greatest height occurring about in the middle and not attaining half the length, both extremities obtusely rounded and nearly equal, dorsal margin very slightly curved, ventral nearly straight; seen dorsally (fig. 6) narrow oblong in form, greatest width only slightly exceeding one-third of the length and occurring behind the middle, both extremities somewhat blunted at the end, the anterior narrower than the posterior. Valves rather pellucid, though not so thin as in *P. reniformis*, and only slightly unequal. Surface of shell smooth, and finely hairy at each extremity. Anterior legs (fig. 8) resembling in structure those in *P. reniformis*, being very coarsely built, with the dactylus strong and abruptly curved at the end. Caudal rami (fig. 9) markedly curved, claws moderately strong and quite smooth, dorsal seta very small.

MALE (fig. 7) of about same size as female, and scarcely differing in the shape of the shell.

Length of shell 0.48 mm., height 0.22 mm., width 0.16 mm.

*Remarks.*—This is a very small species and may easily be recognized by the rather regular elliptical shape of the shell. It is undoubtedly nearest allied to *P. reniformis*, exhibiting a very similar strong development of the anterior legs.

*Occurrence.*—Some few specimens of this form were found in a sample from Tanganyika (138), taken 13/10/04 at Sumbu (S.W. of lake), and a solitary male specimen was found in the same sample (169) in which *P. reniformis* occurred.

9. *PARACYPRIA OPACA*, sp. n. (Plate LXVII. figs. 10-15.)

*Specific Characters.*—FEMALE. Shell moderately compressed; seen laterally (fig. 10) oval in shape, greatest height occurring somewhat in front of the middle and exceeding half the length, both extremities obtusely rounded, the anterior one somewhat broader than the posterior, dorsal margin almost straight in the middle, with slight trace of an angle immediately behind the ocular region, ventral margin very slightly concave in the middle; seen dorsally (fig. 11) oblong in shape, greatest width somewhat exceeding one-third of the length and occurring behind the middle. Valves rather thick and more or less opaque, so as not to allow the limbs to be traced through their walls; left valve, as usual, a little larger than right and overlapping it along the whole anterior extremity, anterior lip of this valve considerably thickened and crossed by a number of somewhat irregular grooves, some of which divide at the end into fine stripes (fig. 13); inner duplicatures of both valves rather broad. Surface of shell of a dull appearance, being sculptured by numerous impressed dots, larger and more distant in the centre of the valves (see fig. 12), very densely crowded in the peripheral parts, where they are partly arranged in curved lines (fig. 10). Anterior legs (fig. 14) less strongly built than in the two preceding species, with the dactylus rather slender and only slightly curved. Caudal rami (fig. 15) almost straight, claws of moderate size, dorsal seta very small.

Length of shell 0.63 mm., height 0.34 mm., width 0.22 mm.

*Remarks.*—By the thick opaque shell with its pronounced sculpture, this form looks very unlike the other species of the genus. On a closer examination of the several appendages, however, I have failed to detect any essential difference in their structure from that of the more typical species, and find it thus impossible to separate this form generically.

*Occurrence.*—Some few female specimens of this species were found in the same sample (138) in which *P. humilis* occurred. Solitary specimens were, moreover, found in two other samples from Tanganyika, the one (82) taken 27/8/04 in Kituta Bay, the other (97), 19/9/04, at Niamkolo, both localities lying at the south end of the lake.

10. *PARACYPRIA CLAVIFORMIS*, sp. n. (Plate LXVIII. figs. 1-10.)

*Specific Characters.*—FEMALE. Shell highly compressed; seen laterally (fig. 1) oblong claviform in shape, greatest height occurring far in front and not attaining half the length, anterior extremity obliquely rounded and somewhat deflexed, posterior much narrower and exserted below to a triangular posteriorly pointing corner, dorsal margin subangular in the ocular region and sloping obliquely behind, being for some extent nearly straight, ventral margin evenly concave in the middle; seen dorsally (fig. 2) narrow fusiform in outline, greatest width not nearly attaining one-third of the length and occurring in the

middle, both extremities acuminate. Valves very thin and pellucid, nearly equal and without any visible pilosity. Surface of shell quite smooth; inner coating exhibiting a faint reticulation, more obvious at the anterior extremity. Muscular impressions in the centre of the valves densely crowded and arranged in the usual manner (fig. 4). Limbs (figs. 5-9) on the whole built upon the same type as in the other species. Caudal rami (fig. 4) unusually short and broad, evenly curved and highly chitinized; claws rather thick and scarcely at all curved, their outer part being clothed inside with fine spinules; dorsal seta well developed.

MALE (fig. 3) of about same size as female, and exhibiting a very similar shape of the shell. Sexual characters developed in the very same manner as in the other species of the genus.

Length of shell 0.58 mm., height 0.28 mm., width 0.17 mm.

*Remarks.*—This is a very distinct species, exhibiting a rather characteristic shape of the shell, and also distinguished by the coarse structure of the caudal rami. It must, however, evidently be regarded as a member of the present genus, as proved by the structure of the several limbs.

*Occurrence.*—Several specimens of this remarkable form, the greater number of them still immature, were picked up from the bottom-residue of a sample from Tanganyika (138), taken 13/10/04 at Sumbu (S.W. of lake). It was not found in any of the other samples.

11. *PARACYPRIA FLEXUOSA*, sp. n. (Plate LXVIII. figs. 11-17.)

*Specific Characters.*—FEMALE. Shell highly compressed, seen laterally (fig. 11) narrow reniform in shape, greatest height occurring about in the middle and not nearly attaining half the length, anterior extremity evenly rounded and conspicuously deflexed, posterior a little narrower and obtuse at the end, dorsal margin only slightly curved, ventral deeply sinuated in front of the middle; seen dorsally (fig. 12) narrow oblong, greatest width scarcely exceeding one-quarter of the length and occurring somewhat behind the middle. Valves rather pellucid and slightly unequal, the right one being somewhat overlapped by the left at the inferior part of both extremities. Surface of shell smooth and shining, without any visible pilosity, but exhibiting a few small dots, more distinct in the anterior part. Eyes of smaller size than in the other species and occurring close to the dorsal margin. Muscular impressions in the centre of the valves (fig. 14) only little differing from those in the other species. Superior antennae (fig. 15) with the setae somewhat reduced in number; natatory setae of the inferior ones apparently likewise less fully developed than usual. Anterior legs (fig. 16) rather slender, with the dactylus comparatively short. Caudal rami (fig. 17) somewhat robust, of equal width throughout, and almost straight; claws comparatively short; dorsal seta very small but distinct, occurring about in the middle of the ramus.

MALE (fig. 13) agreeing with female both in size and in the

shape of the shell, but exhibiting the usual sexual characters, which seem to be fully in accord with those in the other species of the genus.

Length of shell 0.41 mm., height 0.16 mm., width 0.11 mm.

*Remarks.*—I have been in some doubt about the systematic place of this form. In the general shape and sculpturing of the shell, as also in the apparent reduction of the natatory setæ of both pairs of antennæ, it exhibits a certain resemblance to the species of the genus *Candonopsis* Brady, and indeed at first I was inclined to refer it to that genus. On a closer examination of the two solitary specimens found, I now have been induced to abandon this opinion, and find that this form should more properly be referred to the genus *Paracypria*, though constituting a rather anomalous species.

*Occurrence.*—Only two specimens of this small Ostracod, a female and a male, have come under my notice. The female specimen was found in a sample from Tanganyika (138), taken 13/10/04 at Sumbu (S.W. of lake). The male specimen was found in another sample from the same lake (109), taken 28/9/04 at Mbeto (S. end of lake).

## 12. PARACYPRIA CURTA, sp. n. (Plate LXXIII. figs. 15-17.)

*Specific Characters.*—MALE. Shell moderately compressed; seen laterally (fig. 15) of a somewhat triangular form, greatest height occurring a little in front of the middle and exceeding half the length, anterior extremity rather obliquely rounded, posterior narrower and obtuse at the end, dorsal margin considerably arched and sloping behind with a slight curve to the posterior corner, ventral margin slightly concave in the middle; seen dorsally (fig. 16) narrow oblong in form, greatest width somewhat exceeding one-third of the length and occurring behind the middle, both extremities somewhat blunted at the end. Valves thin and pellucid, slightly unequal, and clothed at each extremity with delicate hairs, more densely crowded anteriorly. Surface of shell perfectly smooth. Caudal rami (fig. 17) of quite normal structure, claws rather slender, dorsal seta well developed.

Length of shell 0.55 mm., height 0.30 mm., width 0.20 mm.

*Remarks.*—This is a well-marked genuine *Paracypria*, somewhat resembling in shape *P. complanata*, but of much smaller size and having the shell considerably more abbreviated.

*Occurrence.*—A solitary specimen of this form, a fully grown male, was found in a sample from Tanganyika (138), taken at Sumbu (S.W. of lake).

## Genus 2. CYPRIDORSIS Brady.

Syn. *Candonella* Claus.

*Cypridopsella* Kaufman.

*Remarks.*—This genus was established in the year 1867 by Prof. Brady, to comprise the three northern species, *C. vidua*,



*villosa*, and *aculeata*, and was characterized chiefly by the imperfect development of the caudal rami. In the year 1896 Messrs. Brady and Norman separated one of these species, viz. *C. vidua*, from the other two under a new genus *Pionocypris*, to which they also referred the Australian form described by the present author as *Cypridopsis globulus*. As pointed out by Dr. Vávra, these two species, however, are not congeneric, *P. vidua* having the caudal rami rudimentary, whereas in the Australian species they are normally developed, proving it to belong to the genus *Cypridopsis* of Vávra. The genus *Pionocypris* therefore must be restricted to *P. vidua* and allied European species (*helvetica*, *obesa*, *picta*). I think we are bound to accept the arrangement proposed by the British authors, according to which the type of the genus *Cypridopsis* is not, as suggested by Dr. Vávra and Dr. Kaufman, *C. vidua*, but *C. villosa*, which was referred by Dr. Vávra to the genus *Candonella* Claus, by Dr. Kaufman to his genus *Cypridopsella*.

A third genus, likewise with rudimentary caudal rami, but with reduced natatory setæ on the inferior antennæ, was established by Brady under the name *Potamocypris*. The genus *Paracypridopsis* of Kaufman is in all probability identical with that genus. We have thus three northern generic types, all with rudimentary caudal rami, viz. *Cypridopsis*, *Pionocypris*, and *Potamocypris*, to which recently a fourth African type, *Zonocypris*, has been added by Dr. G. W. Müller. Two species of the last-named genus will be described in the sequel; the other ten species of the "*Cypridopsis*-group" obtained by the Tanganyika Expedition I provisionally refer to the genus *Cypridopsis*, as restricted by Messrs. Brady and Norman.

### 13. CYPRIDOPSIS OBLIQUATA, sp. n. (Plate LXIX. figs. 1-10.)

*Specific Characters*.—FEMALE. Shell moderately tumid; seen laterally (fig. 1) of oval triangular shape, greatest height occurring a little behind the middle and exceeding half the length, both extremities obliquely rounded and nearly equal, dorsal margin strongly arched in the middle, ventral nearly straight; seen dorsally (fig. 2) oblong-ovate in form, greatest width considerably exceeding one-third of the length and occurring a little behind the middle, anterior extremity narrower than posterior. Valves rather pellucid and very conspicuously unequal, the left one being much the larger and overlapping the right, not only anteriorly, but also along the greater part of the dorsal face, whereby the shell assumes a peculiar oblique appearance\*. Surface of shell smooth, but rather densely hairy at each extremity. Muscular impressions in the centre of the valves (fig. 3) somewhat differing in their arrangement from those in the genus *Paracypridopsis*. Eye large and conspicuous. Superior antennæ (fig. 4) of normal structure. Inferior antennæ (fig. 5) rather coarsely built, with the apical

\* It may here be noted that in *C. villosa*, where a similar obliquity of the shell occurs, it is not the left but the right valve which is the larger.

claws strong and partly denticulate inside; natatory setæ issuing at some distance from the end of the second joint and extending about as far as the claws. Mandibular palp (fig. 6) comparatively smaller than in *Paracypria*, with the last joint short and thick. Palp and masticatory lobes of anterior maxillæ (fig. 7) slender and narrow. Anterior legs (fig. 8) comparatively large, with the dactylus strong and evenly curved. Posterior legs (fig. 9) much smaller, and having the reflexed apical seta quite short. Caudal rami (fig. 10) reduced to two small juxtaposed lamellæ of conical form, each terminating in a slender seta and having a small lateral hair. Ends of ovarial tubes, as in most other Cypridæ, ascending along the posterior edges of the valves (fig. 1).

Length of shell 0.53 mm., height 0.30 mm., width 0.22 mm.

*Remarks.*—This form may be easily distinguished from any of the other species here recorded by the peculiar obliquity of the shell, the left valve overlapping conspicuously the right dorsally, in such manner that, in the lateral view of the shell (fig. 1), the line of junction between the valves cuts off, as it were, on the right side a narrow marginal area, extending along the greater part of the dorsal side.

*Occurrence.*—Two or three female specimens of this form were found in the same sample (138) from which *Paracypria curta* was derived. Moreover, a single specimen, likewise of the female sex, was found in another sample from Tanganyika (150), taken 29/10/04 in Vua harbour (W. shore of lake).

14. *CYPRIDOPSIS SINUATA*, sp. n. (Plate LXIX. figs. 11-18.)

*Specific Characters.*—FEMALE. Shell less tumid; seen laterally (fig. 11) of a somewhat reniform shape, greatest height occurring a little in front of the middle and scarcely exceeding half the length, both extremities somewhat obliquely rounded and nearly equal, dorsal margin evenly curved, ventral distinctly sinuated in the middle; seen dorsally (fig. 12) oblong-oval in form, greatest width about equalling two-fifths of the length and occurring somewhat behind the middle, anterior extremity acuminate, posterior more obtuse. Valves rather thin and pellucid, slightly unequal, the left overlapping the right somewhat along the anterior extremity, and at the lower part of the posterior, but not dorsally. Surface of shell smooth and finely hairy at both extremities.

MALE (fig. 13) somewhat smaller than female and slightly differing in the shape of the shell, which is more deeply sinuated below, and has the anterior extremity broader than the posterior and more blunted. Inferior antennæ (fig. 14) of exactly the same structure as in the female, the third joint not being, as in the males of *Paracypria*, subdivided. Prehensile palps of posterior maxillæ (figs. 15 & 16) rather dissimilar on right and left sides, that of right maxilla (fig. 16) having the claw lamella dilated. Copulatory appendages (fig. 17) with the terminal piece securiform in

shape. Ejaculatory tubes (fig. 18) each with eight verticils of chitinous stripes, extremities of tube not dilated.

Length of shell ♀ 0.47 mm., height 0.23 mm., width 0.19 mm.

*Remarks.*—This form is evidently nearly allied to the preceding one, but is of smaller size and differs conspicuously in the shape of the shell, which, moreover, does not exhibit the characteristic obliquity found in that species.

*Occurrence.*—Some few specimens of this form were found in the same sample (138) in which the preceding species occurred, and solitary specimens were found in two other samples from Tanganyika, the one (169) taken 18/11/04 at Kala (E. shore of lake), the other (240) 24/2/05 at Baraka (N.W. shore).

15. *CYPRIDOPSIS CUNNINGTONI*, sp. n. (Plate LXX. figs. 1-3.)

*Specific Characters.*—FEMALE. Shell rather compressed; seen laterally (fig. 1) of a somewhat trigonal form, greatest height occurring a little in front of the middle and considerably exceeding half the length, anterior extremity rounded, posterior much narrower and terminating below in an obtuse corner, dorsal margin strongly arched in the middle, ventral one slightly sinuated; seen dorsally (fig. 2) narrow oblong in form, greatest width about equalling one-third of the length and occurring in the middle, both extremities acuminate. Valves rather thin and nearly equal, finely hairy at both extremities. Surface of shell smooth.

MALE (fig. 3) of somewhat larger size than female, and having the shell more deeply sinuated ventrally, with the posterior extremity narrower and more deflexed.

Length of shell ♀ 0.56 mm., height 0.32 mm., width 0.20 mm.

*Remarks.*—This is a quite genuine *Cypridopsis*, resembling somewhat in shape the type species, *C. villosa* Jurine, but having the shell less densely pilose and the valves much less unequal, without any obvious obliquity of the shell. It is the largest of the species here recorded.

*Occurrence.*—Two specimens only of this form, a female and a male, have come under my notice. They were derived from a sample (14) taken 17/6/04 in Monkey Bay, Lake Nyasa, and had been separated by Dr. Cunningham in a small tube. I therefore find it appropriate to name this species in honour of the distinguished conductor of the Expedition.

16. *CYPRIDOPSIS PUSILLA*, sp. n. (Plate LXX. figs. 4-6.)

*Specific Characters.*—FEMALE. Shell moderately compressed; seen laterally (fig. 4) oval in form, greatest height occurring a little behind the middle and equalling about half the length, both extremities obtusely rounded and slightly deflexed, nearly equal, dorsal margin somewhat irregularly curved, ventral almost straight; seen dorsally (fig. 5) oblong in form, greatest width about equalling two-fifths of the length and occurring in the middle, both extremities somewhat blunted at the end. Valves

rather thin and pellucid, slightly unequal, and finely hairy at each extremity. Surface of shell perfectly smooth.

MALE (fig. 6) somewhat smaller than female, but exhibiting a very similar shape of the shell.

Length of shell ♀ 0.41 mm., height 0.21 mm., width 0.17 mm.

*Remarks.*—This form is allied to *C. sinuata*, but of rather smaller size, and differs conspicuously in the nearly straight ventral margin of the shell.

*Occurrence.*—Some few specimens of this small Ostracod were found in a sample from Tanganyika (138), taken 13/10/04 at Sumbu (S.W. of lake).

17. *CYPRIDOPSIS MONODONTA*, sp. n. (Plate LXX. figs. 7-9.)

*Specific Characters.*—MALE. Shell somewhat tumid; seen laterally (fig. 7) almost semicircular in outline, greatest height occurring in the middle and nearly attaining two-thirds of the length, anterior extremity obliquely rounded, posterior blunted and somewhat deflexed, dorsal margin boldly arched, ventral nearly straight; seen dorsally (fig. 8) subovate in form, greatest width exceeding half the length and occurring behind the middle, both extremities somewhat blunted at the end, the posterior one being the broader. Valves rather unequal, the left one overlapping the right conspicuously along the whole anterior extremity, anterior lip of this valve somewhat deflexed and having below a slight sinus; posterior lip armed at the lower corner with a small recurved dentiform process (fig. 9). Surface of shell smooth, but rather densely hairy at both extremities.

Length of shell ♀ 0.36 mm., height 0.23 mm., width 0.20 mm.

*Remarks.*—This is the smallest of all the Tanganyika Ostracoda, and is, moreover, easily recognized by the short and tumid shell and by the peculiar dentiform process springing off from the posterior corner of the left valve, a character which has given rise to the specific name here proposed.

*Occurrence.*—A solitary male specimen of this form was found in the same sample (138) from which *C. pusilla* was derived.

18. *CYPRIDOPSIS SERRATA*, sp. n. (Plate LXX. figs. 10-12.)

*Specific Characters.*—FEMALE. Shell moderately tumid; seen laterally (fig. 10) oblong reniform in shape, greatest height occurring in the middle and about equalling half the length, both extremities obliquely rounded and somewhat deflexed, dorsal margin evenly curved, ventral conspicuously sinuated; seen dorsally (fig. 11) oblong-ovate in form, greatest width about equalling two-fifths of the length and occurring behind the middle, both extremities acuminate. Valves rather unequal, the right being conspicuously overlapped by the left, both anteriorly and posteriorly; each valve exhibiting at the posterior corner a row of extremely delicate triangular serrations, four on right, three on left valve (fig. 12). Surface of shell smooth and finely hairy at both extremities.

Length of shell 0.52 mm., height 0.26 mm., width 0.21 mm.

*Remarks.*—This form may be easily recognized by its comparatively narrow reniform shell, and more particularly by the peculiar delicate serrations occurring on the posterior corners of both valves, a character from which the specific name here proposed has been derived.

*Occurrence.*—Of this species also only a single specimen has been secured, a fully grown female. It was found in a sample from Tanganyika (169), taken 18/11/04 at Kala (E. shore of lake).

19. *CYPRIDOPSIS BIDENTATA*, sp. n. (Plate LXXI. figs. 1-3.)

*Specific Characters.*—FEMALE. Shell moderately tumid; seen laterally (fig. 1) rounded triangular in shape, greatest height occurring in the middle and considerably exceeding half the length, both extremities obliquely rounded and somewhat deflexed, the posterior one more blunted than the anterior, dorsal margin boldly arched and sloping more steeply to the anterior than to the posterior extremity, ventral margin nearly straight; seen dorsally (fig. 2) subovate in form, greatest width about half the length and occurring behind the middle, anterior extremity narrower than posterior. Valves slightly unequal, the left overlapping the right along the anterior extremity, as also at the lower part of the posterior one, hind corner of this valve armed with two recurved dentiform processes (fig. 3) similar to that found in *C. monodonta*. Surface of shell smooth, but rather densely hairy at each extremity.

MALE of about same size as female and exhibiting a similar shape and armature of the shell.

Length of shell 0.49 mm., height 0.29 mm., width 0.23 mm.

*Remarks.*—This form somewhat resembles *C. monodonta* in the shape and armature of the shell, but is of considerably larger size, and is, moreover, distinguished by the presence of two dentiform processes, instead of a single one, at the posterior corner of the left valve.

*Occurrence.*—Two specimens of this form, a male and a female, were found in a sample from Tanganyika (97), taken 19/9/04 at Niamkolo (S. end of lake).

20. *CYPRIDOPSIS TUMIDULA*, sp. n. (Plate LXXI. figs. 4-6.)

*Specific Characters.*—FEMALE. Shell unusually tumid; seen laterally (fig. 4) of oval reniform shape, greatest height occurring somewhat in front of the middle and scarcely exceeding half the length; anterior extremity obliquely rounded, posterior scarcely narrower and blunted at the end; dorsal margin somewhat irregularly curved, sloping more steeply in front than behind, ventral margin distinctly concave in the middle: seen dorsally (fig. 5) ovate in form, greatest height exceeding half the length and occurring about in the middle, anterior extremity narrower than posterior. Valves rather unequal, the left one considerably over-

lapping the right along the anterior extremity as also somewhat along the lower part of the posterior, hind corner of this valve armed with two delicate triangular teeth, that of right valve with a single such tooth placed somewhat farther above (fig. 6). Surface of shell smooth, but rather densely hairy at both extremities.

Length of shell 0.47 mm., height 0.24 mm., width 0.25 mm.

*Remarks.*—This form may at once be distinguished from any of the other species here recorded by the unusually tumid shell, the width of which even somewhat exceeds the height. The armature of the hind corner of each valve is also characteristic.

*Occurrence.*—A solitary female specimen of this form was found in a sample from Tanganyika (138), taken 13/10/04 at Sumbu (S.W. of lake).

## 21. CYPRIDOPSIS CONGENERA, sp. n. (Plate LXXI. figs. 7-9.)

*Specific Characters.*—FEMALE. Shell moderately tumid; seen laterally (fig. 7) of oval reniform shape, greatest height occurring about in the middle and slightly exceeding half the length, both extremities rounded and slightly deflexed, dorsal margin irregularly curved, with trace of an angle behind the ocular region, ventral margin very slightly concave in the middle; seen dorsally (fig. 8) oblong-ovate in form, greatest width occurring behind the middle and not attaining half the length, anterior extremity acuminate, posterior blunted. Valves slightly unequal, left valve overlapping the right somewhat along the anterior extremity, but scarcely behind. Surface of shell smooth and finely hairy at both extremities.

MALE (fig. 9) a little smaller than female and having the posterior extremity of the shell somewhat narrower.

Length of shell 0.52 mm., height 0.28 mm., width 0.23 mm.

*Remarks.*—This form is closely allied to *C. sinuata*, exhibiting a rather similar shape of the shell. It is, however, of larger size and has the ventral margin of the shell much less sinuated.

*Occurrence.*—Three specimens of this form, two females and one male, were found in the same sample from which *C. tumidula* was derived.

## 22. CYPRIDOPSIS GIBBA, sp. n. (Plate LXXI. figs. 10-12.)

*Specific Characters.*—FEMALE. Shell somewhat compressed; seen laterally (fig. 10) of oval trigonal shape, greatest height occurring about in the middle and exceeding half the length, anterior extremity broadly rounded, posterior somewhat narrower and blunted at the end; dorsal margin forming in the middle an abrupt angular curve and sloping from thence evenly to each extremity, ventral margin exhibiting in the middle a distinct sinus, in front of which is a slight convexity: seen dorsally (fig. 11) oblong-ovate in shape, greatest width not nearly attaining half the length and occurring about in the middle, anterior

extremity acuminate, posterior blunted. Valves rather thin and pellucid, slightly unequal, the left overlapping the right in front and partly also behind by a narrow hyaline border. Surface of shell smooth with only very slight traces of pilosity.

MALE (fig. 12) of nearly same size as female and scarcely differing in the shape of the shell. Sexual characters, however, easily observable in the dense coils of spermatie tubes occurring in the posterior part of each valve, and in the translucent ejaculatory tubes. The latter with numerous (up to 14) whorls of densely crowded chitinous stripes. Copulatory appendages of a similar structure to that in the male of *C. sinuata*, but with the terminal pieces distinctly bilobed.

Length of shell 0.60 mm., height 0.34 mm., width 0.24 mm.

*Remarks.*—This form, like *C. cunningtoni*, is undoubtedly a genuine *Cypridopsis*. It differs from that species, as also from the two African species described by Dr. Vávra and Dr. Müller, in the shape of the shell and in the imperfect pilosity of the same.

*Occurrence.*—Some few specimens of this form were found in a sample from Victoria Nyanza (269), taken 25/4/05 at Bukoba (W. shore of lake).

### Genus 3. ZONOCYPRIS Müller.

*Remarks.*—This genus was established in the year 1898 by Dr. G. W. Müller to comprise two African species, *Z. madagascariensis* and *Z. elegans*, both of which were distinguished by a very peculiar sculpture of the shell, a character which has given rise to the generic name proposed by Dr. Müller. The genus is nearly allied to *Cypridopsis* or still more to *Pionocypris*, but differs in some points from both these genera, and can well be retained. Two species referable to this genus are described below.

#### 23. ZONOCYPRIS COSTATA Vávra. (Plate LXXII, figs. 1-3.)

*Cypridopsis costata* Vávra, Die Süsswasser Ostracoden Deutsch-Ost-Afrikas, p. 10, figs. 1-8.

Syn.: *Zonocypris madagascariensis* Müller.

*Specific Characters.*—FEMALE. Shell very tumid; seen laterally (fig. 1) of a somewhat rhomboidal shape, greatest height occurring a little in front of the middle and slightly exceeding half the length, anterior extremity rounded, posterior obliquely truncated, dorsal margin forming a rather even curve, ventral margin slightly sinuated in the middle; seen dorsally (fig. 2) broadly oviform in shape, greatest width exceeding two-thirds of the length and occurring behind the middle, anterior extremity much narrower than posterior. Valves slightly unequal, the left overlapping the right somewhat along the anterior extremity, as also a little at the upper corner of the posterior one; anterior lips of both valves somewhat thickened, but with only slight trace of hairs. Surface of shell sculptured with very conspicuous elevated ridges arranged

in a concentric manner. Inferior antennæ rather coarsely built, with one of the terminal claws knife-shaped and denticulated along the inner edge (fig. 3). The other limbs resembling in structure those in *Cypridopsis*.

MALE of about same size as female, and exhibiting a very similar shape and sculpture of the shell.

Length of shell 0.60 mm., height 0.32 mm., width 0.39 mm.

*Remarks.*—I cannot see any essential difference between the form described by Dr. Müller as the type of this genus, *Z. madagascariensis*, and the form recorded by Dr. Vávra as *Cypridopsis costata*. Both these forms seem indeed to be identical, and as the specific name proposed by Dr. Vávra is the older one, it ought to be retained for the present species.

*Occurrence.*—Some few specimens of this form were found in a sample from Victoria Nyanza (269), taken 25.4.05 at Bukoba (W. shore of lake).

*Distribution.*—Ugogo, East Africa (Vávra), Madagascar (Müller).

24. ZONOCYPRIS LEVIS, sp. n. (Plate LXXII. figs. 4-7.)

*Specific Characters.*—FEMALE. Shell very tumid; seen laterally (fig. 4) of a somewhat trigonal shape, greatest height occurring about in the middle and considerably exceeding half the length; anterior extremity somewhat obliquely rounded, posterior obliquely truncated below; dorsal margin forming in the middle an abrupt, almost angular curve, ventral margin rather deeply sinuated in the middle: seen dorsally (fig. 5) of regular oviform shape, greatest width equalling two-thirds of the length and occurring behind the middle, anterior extremity much narrower than the posterior. Valves rather thin and pellucid, nearly equal, and clothed at each extremity with delicate hairs. Surface of shell perfectly smooth, without any trace of the concentric ridges found in the preceding species. Muscular impressions in the centre of each valve (fig. 6) densely crowded and somewhat differing in form and arrangement from those in the two preceding genera. Inferior antennæ of much the same structure as in *Z. costata*, one of the apical claws exhibiting a very similar knife-like shape and coarse denticulation of the inner edge (fig. 7).

Length of shell 0.58 mm., height 0.33 mm., width 0.37 mm.

*Remarks.*—The above-described form is unquestionably congeneric with the preceding species, agreeing with it in all essential structural details. Yet it differs very conspicuously in even the character from which the present genus has been named, the surface of the shell being perfectly smooth, without the slightest trace of any sculpturing. The generic name proposed by Dr. Müller, of course, is somewhat inappropriate, since it does not apply to all the species.

*Occurrence.*—Some specimens of this form, most of them not in a good state of preservation, were found together with *Z. costata* in the above-mentioned sample from Victoria Nyanza.



## Genus 4. STENOCYPRIS G. O. Sars.

*Remarks.*—The type of this genus is *S. malcolmsoni* Brady, of which a detailed description has been given by the present author from Australian specimens. The most prominent character distinguishing this genus is unquestionably the peculiar asymmetry of the caudal rami, the right one of which is much coarser than the left and armed along the dorsal edge with a comb-like series of strong denticles, wanting or only slightly indicated on the left ramus. This character is found in several other species recently described by Dr. Vávra and Dr. Müller, and may thus prove to be a very good generic criterion. The form recorded by the present author as *Stenocypris chevreuxi*, in which such an asymmetry does not exist, I am now inclined to refer to the genus *Herpetocypris*, in spite of the presence in this form of distinct, though very short natatory setæ on the inferior antennæ. In all other characters this form exhibits a much closer relationship to the genus *Herpetocypris* than to *Stenocypris*. A genuine species of the present genus is described below.

## 25. STENOCYPRIS PERARMATA Brady. (Plate LXXII. figs. 8-10.)

*Stenocypris perarmata* Brady, Entomostraca collected in Natal by Mr. J. Gibson, Proc. Zool. Soc. Lond. 1904, vol. ii. p. 126, pl. viii. figs. 50-57.

*Specific Characters.*—FEMALE. Shell much compressed; seen laterally (fig. 8) of elongated siliquose shape, greatest height occurring behind the middle and only slightly exceeding one-third of the length; anterior extremity somewhat obliquely rounded, posterior narrower and obtuse at the end, none of the extremities deflexed; dorsal margin gently curved, sloping evenly towards the anterior extremity, more steeply towards the posterior, above which there is trace of a slight concavity; ventral margin exhibiting in front of the middle a slight sinus bounded anteriorly (in the oral region) by a small convexity: seen dorsally (fig. 9) narrow oblong in form, with the greatest width only slightly exceeding one-quarter of the length, both extremities acuminate. Valves thin and pellucid, only slightly unequal, the left overlapping a little the right along the anterior extremity and also somewhat behind. Surface of shell smooth, but rather densely hairy both at the extremities and below. Caudal rami (fig. 10) exhibiting the structure characteristic of the genus; right ramus conspicuously broader than the left and armed on the distal part of the dorsal edge with a row of about eight coarse teeth, followed by a number of smaller and somewhat unequal denticles; dorsal edge of left ramus with only very small hair-like denticles in its outermost part; apical claws of both rami rather strong and somewhat unequal, the distal one being much the longer, though scarcely exceeding half the length of the ramus; both claws coarsely denticulated along the greater part of the concave edge, seta of

dorsal edge wanting, apical seta rather slender, extending almost as far as the distal claw.

Length of shell 1.48 mm., height 0.60 mm., width 0.41 mm.

*Remarks.*—I think I am right in identifying the present form with that described by Brady under the above name, though some small differences as to the shape of the shell may be found on comparing the figures here given with those reproduced by Prof. Brady.

*Occurrence.*—A nearly adult female specimen (that here figured) of this form had been mounted by Dr. Cunningham on a slide, together with some other Entomostraca. According to the label, they were derived from amongst algæ taken 23/6/04 in Nkata Bay on the west coast of Lake Nyasa. Another somewhat smaller specimen of the same species, likewise mounted, was found in Tanganyika, the exact locality not being stated.

*Distribution.*—Natal (*Brady*).

#### Genus 5. HETEROCYPRIS Claus.

*Remarks.*—According to Dr. Vávra, a genus with the above name was established by Claus in the year 1892, to include the well-known northern species, *Cypris incongruens* Ramdohr. Dr. Vávra considers this genus as constituting only a subsection of the genus *Cyprinotus* Brady. As, however, both these subsections are rather well defined and comprise at present each a number of species, I find it more appropriate to maintain the genus in Claus' form. A third closely allied genus is the one established by the present author as *Hemicypris*, to include *Cypris pyxidata* Moniez and allied species. The following species is only provisionally referred to the genus of Claus.

#### 26. HETEROCYPRIS DUBIA, sp. n. (Plate LXXII. figs. 11-14.)

*Specific Characters.*—FEMALE. Shell somewhat compressed; seen laterally (fig. 11) of oval reniform shape, greatest height occurring behind the middle and exceeding half the length, anterior extremity narrowly rounded, posterior much broader and obtusely blunted; dorsal margin sloping with an even curve to the anterior extremity, abruptly deflexed behind, ventral margin somewhat convex behind and very slightly sinuated in front of the middle: seen dorsally (fig. 12) oblong-oval in form, greatest width equalling about two-fifths of the length and occurring in the middle, both extremities somewhat blunted. Valves very thin and pellucid, slightly unequal, the left one overlapping the right a little in front and also somewhat along the posterior half of the ventral face; lips of both valves perfectly smooth, without any trace of the crenulation found in other species of this and allied genera. Surface of shell smooth and clothed at both extremities with very delicate hairs. Muscular impressions in the centre of each valve (fig. 13) five in number and arranged in the usual manner

Caudal rami (fig. 14) rather narrow, nearly straight, and slightly tapering distally, dorsal edge perfectly smooth; apical claws of moderate size and somewhat unequal, the distal one the longer and about equalling in length half the ramus; dorsal seta shorter than the proximal claw and attached at only a short distance from it, apical seta very small.

Length of shell 0.86 mm., height 0.48 mm., width 0.36 mm.

*Remarks.*—In the shape of the shell, as seen laterally, this form looks rather like the African species described by Dr. Vávra as *Cyprinotus fossulatus*. It is, however, of smaller size and far less tumid, exhibiting, moreover, no trace of the impressed dots with which the surface of the shell in that species is sculptured, nor have I been enabled to detect any tubercles on the edges of the valves. In so far this form differs materially from any of the other known species. In the structure of the several appendages, however, as far as these could be examined in the solitary specimen found, no essential differences could be traced.

*Occurrence.*—A solitary female specimen of this form was found in a sample from Victoria Nyanza (250), taken 20/4/05 at Bukoba (W. shore of lake).

#### Genus 6. ILYOCYPRIS Brady.

*Remarks.*—Several northern species of this distinct genus have been described, and also an Australian species, *I. australis* G. O. Sars. In the Ostracod material from the Tanganyika Expedition two species of this genus are represented, though only by solitary specimens. I have been unable to identify either of them with previously described species.

#### 27. ILYOCYPRIS PROPINQUA, sp. n. (Plate LXXIII. figs. 1-4.)

*Specific Characters.*—FEMALE. Shell moderately compressed; seen laterally (fig. 1) of oval reniform shape, greatest height occurring far in front and slightly exceeding half the length, anterior extremity broadly rounded, posterior narrower and obtusely truncated; dorsal margin nearly straight and obliquely sloping behind, forming with the posterior margin an obtuse angle, ventral margin deeply sinuated in the middle: seen dorsally (fig. 2) oblong-ovate in form, projecting on each side behind the middle to an obtuse protuberance, another smaller rounded prominence occurring on each side in front of the middle. Valves only slightly pellucid and somewhat unequal, the right overlapping the left in front by a narrow hyaline rim, and also somewhat along the posterior part of the ventral face. Surface of shell sculptured with densely crowded impressed dots and provided with scattered stiff hairs, more conspicuous at each extremity. Muscular impressions in the centre of each valve (fig. 3) densely crowded and somewhat differing in number and arrangement from those in the other genera. Caudal rami (fig. 4) rather narrow and conspicuously curved, dorsal edge smooth; apical claws rather slender.

and somewhat unequal, the distal one being much the longer and considerably exceeding half the length of the ramus; seta of dorsal edge well developed.

Length of shell 0.94 mm., height 0.50 mm., width across the posterior protuberances 0.40 mm.

*Remarks.*—This form somewhat resembles the northern species *I. gibba* Ramdohr, exhibiting a rather similar shape of the shell, which, as in that species, is produced on each side behind the middle to a well-marked protuberance; but these protuberances are in the present species considerably broader and more obtuse at the tip, more resembling those in the Chinese species *I. angulata* G. O. Sars. The structure of the caudal rami is also somewhat different.

*Occurrence.*—A solitary female specimen of this form was found in a sample from Lake Nyasa (8), taken 11/6/04 in Anchorage Bay (S. end of lake).

28. *ILYOCYPRIS ALTA*, sp. n. (Plate LXXIII. figs. 5-7.)

*Specific Characters.*—**MALE.** Shell less compressed than in the preceding species, seen laterally (fig. 5) of a somewhat clavate shape, greatest height occurring far in front and exceeding three-fifths of the length, anterior extremity very broad and amply rounded, posterior much narrower and blunted at the end; dorsal margin forming in the ocular region an abrupt angular bend and sloping thence rather steeply behind, joining the posterior margin at an obtuse angle, ventral margin deeply sinuated in the middle: seen dorsally (fig. 6) of irregular oblong-ovate form, exhibiting, as in the preceding species, on each side in front of the middle a rounded tuberculiform prominence, and farther behind a broad obtuse protuberance, below which another somewhat smaller protuberance occurs. Valves rather thin and pellucid, conspicuously unequal, the right one overlapping the left in front by a rather broad hyaline rim, as also somewhat behind. Surface of shell less distinctly dotted and clothed with scattered delicate hairs. Caudal rami (fig. 7) comparatively shorter and stouter than in the preceding species and less curved, apical claws nearly equal in length, dorsal seta comparatively small.

Length of shell 0.80 mm., height 0.51 mm., width across the posterior protuberances 0.40 mm.

*Remarks.*—This form is unquestionably specifically distinct from the preceding one, differing rather conspicuously both from this and the other known species in the shape of the shell, as also in the structure of the caudal rami.

*Occurrence.*—Of this form also only a solitary specimen has come under my notice. It had been separated by Dr. Cunningham in a small tube, and proved, on a closer examination, to be a nearly adult male. According to the label it was found in a sample from Tanganyika (169) taken 18/11/04 at Kala (E. shore of lake).

## Family CYTHERIDÆ.

## Genus 7. LIMNICYTHERE Brady.

*Remarks.*—Of this genus, which exhibits so close a relationship to true marine Ostracoda, four or five northern species have been described, all of which are found exclusively in freshwater ponds or lakes. No species of this genus is, however, as yet known from the Southern Hemisphere. In the Ostracod material of the Tanganyika Expedition one species referable to this genus is represented, and another nearly related African species is known to me, having been found in a sample taken by Dr. Purcell from a freshwater pond in Cape Colony.

## 29. LIMNICYTHERE OBTUSATA, sp. n. (Plate LXXIII. figs. 8-14.)

*Specific Characters.*—FEMALE. Shell rather tumid; seen laterally (fig. 8) of regular oblong-oval shape, greatest height scarcely attaining half the length, both extremities obtusely rounded and of about same breadth; dorsal margin straight and horizontal, forming in front, just above the eye, an abrupt angular bend, ventral margin very slightly concave in front of the middle: seen dorsally (fig. 9) irregularly subovate in shape, being conspicuously constricted in front of the middle and bulging behind, greatest width almost attaining two-thirds of the length and occurring in the posterior part, anterior extremity acuminate, posterior blunted. Dorsal face of shell somewhat fornicate, ventral flattened, the greatest convexity of the shell occurring far below. Valves rather thin and flexible, being very little calcified and slightly unequal, the left valve overlapping the right a little in front, but scarcely behind. Surface of shell of a dull appearance, being distinctly reticulated, and clothed at both extremities with stiff hairs, more densely crowded along the anterior one. Muscular impressions in the centre of each valve (fig. 10) four in number and arranged in a regular vertical series. Eye single, not, as in the marine Cytheridæ, double. Superior antennæ (fig. 11) rather stout, being composed of six well-defined joints, the first two of which are much the largest and forming together a geniculate bend; setæ of the terminal part short, partly spiniform. Inferior antennæ (fig. 12) 4-articulate, without any trace of natatory setæ, but with a strong deflexed, biarticulate spine issuing from the end of the basal joint and extending beyond the apical claws, the latter comparatively short and only three in number. Mandibles and maxillæ of normal structure. The three pairs of legs (fig. 13) gradually increasing in length and of comparatively simple structure, each carrying on the end a strong claw, that of last pair, however, more slender. Caudal lobes (fig. 14) rather broad, and each provided with four thick and densely ciliated setæ.

Length of shell 0.60 mm., height 0.30 mm., width 0.38 mm.

*Remarks.*—This form differs conspicuously in the shape of the shell from any of the northern species, and more resembles in this

respect the South American form recently described by Dr. Daday as *Cypridinella ilosvagi*. The structure of the legs and the caudal lobes is, however, very different, and on the whole in accord with that found in the species of the present genus.

*Occurrence.*—Some few female specimens of this form, most of them not in a good state of preservation, were found in a sample from Victoria Nyanza (269), taken 25/4/05 at Bukoba (W. shore of lake).

#### GENERAL REMARKS.

The occurrence of Ostracoda in the samples taken by Dr. Cunningham during the Tanganyika Expedition must on the whole be regarded as a very unexpected circumstance, since these samples, as a rule, were all taken at the very surface by the aid of a fine-meshed tow-net. None of the known freshwater Ostracoda are, however, limnetic in habits, such as is the case with many of the Copepoda and Cladocera. They all are true bottom animals, though some of them are enabled, by the aid of the natatory setæ attached to the antennæ, to move freely in the water to some extent. The occurrence of specimens of this group in the samples may therefore be regarded as quite accidental, chiefly caused by the circumstance that in some cases the samples have been taken in quite shallow parts of the lakes, whereby some parcels of the bottom material have happened to be introduced in the tow-net\*. The great number of species determined is still more perplexing and could easily lead to the wrong supposition that the Ostracod material procured was a very large and extensive one. This is, however, by no means the case. The material is in reality, as to quantity, very small, only one or two of the species being represented by a tolerably great number of individuals, all the others only by quite solitary specimens. Although the present account, therefore, in all probability, only gives a slight glimpse into the Ostracodous fauna of the three great Central African lakes, it will, I think, suffice to again emphasize the peculiar faunistic character of Lake Tanganyika, as compared with the other two lakes. A glance at the annexed table of distribution will show that the far greater number of species are derived from that lake, and the contrast between Tanganyika and the other two lakes is, in this case, even more striking than in the case of the Copepoda, no less than 22 species occurring in Tanganyika, whereas only three species are found in Lake Nyasa and five species in Victoria Nyanza. It will, moreover, be seen that at the same time only a single species, *Stenocypris perarmata*, occurs in two of the lakes (Tanganyika and Nyasa); in all other cases the species of the three lakes are different. Two

\* Dr. Cunningham has recently called my attention to the fact that several of the samples, and in particular those which turned out to be most productive in Ostracoda, were taken during the night; and he has suggested that their occurrence in the surface-gatherings may more properly be explained by the very probable assumption that freshwater Ostracoda, like many marine bottom-crustacea, rise to the surface after dark.

Table of Distribution.

Names of Species.	Tanganyika.	Nyasa.	Victoria Nyanza.	Other parts of Africa.
<i>Paracyprina declivis</i> G. O. S. ....	+			
" <i>complanata</i> G. O. S. ....	+			
" <i>canoidea</i> G. O. S. ....	+			
" <i>obtus</i> G. O. S. ....	+			
" <i>depressa</i> G. O. S. ....	+			
" <i>subangulata</i> G. O. S. ....	+			
" <i>reniformis</i> G. O. S. ....	+			
" <i>humilis</i> G. O. S. ....	+			
" <i>opaca</i> G. O. S. ....	+			
" <i>claviformis</i> G. O. S. ....	+			
" <i>flexuosa</i> G. O. S. ....	+			
" <i>curta</i> G. O. S. ....	+			
<i>Cypridopsis obliquata</i> G. O. S. ....	+			
" <i>sinuata</i> G. O. S. ....	+			
" <i>cunningtoni</i> G. O. S. ....		+		
" <i>pusilla</i> G. O. S. ....	+			
" <i>monodonta</i> G. O. S. ....	+			
" <i>serrata</i> G. O. S. ....	+			
" <i>bidentata</i> G. O. S. ....	+			
" <i>tumidula</i> G. O. S. ....	+			
" <i>congenera</i> G. O. S. ....	+			
" <i>gibba</i> G. O. S. ....			+	
<i>Zonocypris costata</i> Fädra ....			+	+
" <i>bavis</i> G. O. S. ....			+	
<i>Stenocypris perarmata</i> Brady ....	+	+		+
<i>Heterocypris dubia</i> G. O. S. ....			+	
<i>Nyocypris propinqua</i> G. O. S. ....		+		
" <i>alta</i> G. O. S. ....	1			
<i>Limnocythere obtusata</i> G. O. S. ....			+	
29 species.	22	3	5	2

of the genera here recorded are especially richly represented in Lake Tanganyika, viz. *Paracyprina* and *Cypridopsis*. Of the first-named genus no less than twelve different species have been determined, all exclusively peculiar to that lake and exhibiting a remarkable specialisation as regards the external appearance. The type of this genus, *P. tenuis* G. O. S., as mentioned above, was found in the very same brackish-water lagoon on the Chatham Islands from which the type of the Copepod genus *Schizopera* was derived. The suggestions set forth in my previous paper about the probable origin of the several species of the last-named genus occurring in Tanganyika may therefore also apply to those of the Ostracod genus here under question. As regards the other genus, *Cypridopsis*, it may be noted here that only two of the ten species determined exhibit all the characteristic features of that genus, and these two species do not occur in Tanganyika, one of them, *C. cunningtoni*, being derived from Lake Nyasa, the other, *C. gibba*, from Victoria Nyanza. The remaining eight species differ somewhat in the shape of the shell and the mutual

relation of the two valves, as also apparently in the structure of the ejaculatory tubes in the male, and should perhaps more properly be combined into a separate new genus, which, in such case, would be exclusively peculiar to Lake Tanganyika.

## EXPLANATION OF THE PLATES.

## PLATE LXIV.

*Paracyprina declivis* G. O. Sars.

- Fig. 1. Adult female, viewed from right side.  
2. Same, dorsal view.  
3. Adult male, seen from left side.  
4. Anterior leg.  
5. Posterior leg.  
6. Caudal ramus.  
7. Palp of left posterior maxilla of male.  
8. Palp of right posterior maxilla of same.

*Paracyprina complanata* G. O. Sars.

- Fig. 9. Adult male, viewed from right side.  
10. Same, dorsal view.

*Paracyprina conoidea* G. O. Sars.

- Fig. 11. Adult male, viewed from right side.  
12. Same, dorsal view.

## PLATE LXV.

*Paracyprina obtusa* G. O. Sars.

- Fig. 1. Adult female, viewed from right side.  
2. Same, dorsal view.  
3. Adult male, viewed from left side.  
4. Piece of the central part of right valve, showing the finely striated sculpture of the shell and the group of muscular impressions.  
5. Superior antenna.  
6. Inferior antenna.  
7. Mandible and palp.  
8. Anterior maxilla with vibratory plate.  
9. Posterior maxilla.  
10. Anterior leg.  
11. Posterior leg.  
12. Caudal ramus.  
13. Inferior antenna of male.  
14. Palp of right posterior maxilla of same.  
15. Palp of left posterior maxilla of same.  
16. Copulatory appendage of same.  
17. Ejaculatory tube of same.

## PLATE LXVI.

*Paracyprina deflexa* G. O. Sars.

- Fig. 1. Adult female, viewed from right side.  
2. Same, dorsal view.  
3. Adult male, viewed from left side.  
4. Anterior lips of valves, viewed from right side.  
5. Piece of the central part of right valve, showing the muscular impressions.  
6. Caudal ramus.

*Paracyprina subangulata* G. O. Sars.

- Fig. 7. Adult female, viewed from right side.  
8. Same, dorsal view.  
9. Adult male, viewed from left side.  
10. Anterior lips of valves, viewed from right side.  
11. Caudal ramus.



## PLATE LXVII.

*Paracypria reniformis* G. O. Sars.

- Fig. 1. Adult female, viewed from right side.  
 2. Same, dorsal view.  
 3. Anterior leg.  
 4. Caudal ramus.

*Paracypria humilis* G. O. Sars.

- Fig. 5. Adult female, viewed from right side.  
 6. Same, dorsal view.  
 7. Adult male, viewed from left side.  
 8. Anterior leg.  
 9. Caudal ramus.

*Paracypria opaca* G. O. Sars.

- Fig. 10. Adult female, viewed from right side.  
 11. Same, dorsal view.  
 12. Piece from the central part of right valve, showing the sculpture of the shell and the muscular impressions.  
 13. Anterior lip of left valve, viewed from the inner side.  
 14. Anterior leg.  
 15. Caudal ramus.

## PLATE LXVIII.

*Paracypria claviformis* G. O. Sars.

- Fig. 1. Adult female, viewed from right side.  
 2. Same, dorsal view.  
 3. Adult male, viewed from left side.  
 4. Piece from the central part of right valve, showing the muscular impressions.  
 5. Superior antenna.  
 6. Inferior antenna.  
 7. Anterior maxilla, without the vibratory plate.  
 8. Anterior leg.  
 9. Posterior leg.  
 10. Caudal ramus.

*Paracypria flexuosa* G. O. Sars.

- Fig. 11. Adult female, viewed from left side.  
 12. Same, dorsal view.  
 13. Adult male, viewed from right side.  
 14. Piece from the central part of right valve, showing the muscular impressions.  
 15. Superior antenna.  
 16. Anterior leg.  
 17. Caudal ramus.

## PLATE LXIX.

*Cypridopsis obliquata* G. O. Sars.

- Fig. 1. Adult female, viewed from right side.  
 2. Same, dorsal view.  
 3. Muscular impressions of right valve.  
 4. Superior antenna.  
 5. Inferior antenna.  
 6. Mandible and palp.  
 7. Anterior maxilla, without the vibratory plate.  
 8. Anterior leg.  
 9. Posterior leg.  
 10. Caudal ramus.

*Cypridopsis sinuata* G. O. Sars.

- Fig. 11. Adult female, viewed from right side.  
 12. Same, dorsal view.  
 13. Adult male, viewed from left side.  
 14. Inferior antenna of male.  
 15. Palp of left posterior maxilla of same.  
 16. Right posterior maxilla of same.  
 17. Copulatory appendages of same.  
 18. Ejaculatory tube.

## PLATE LXX.

*Cypridopsis cunningtoni* G. O. Sars.

- Fig. 1. Adult female, viewed from right side.  
 2. Same, dorsal view.  
 3. Adult male, viewed from left side.

*Cypridopsis pusilla* G. O. Sars.

- Fig. 4. Adult female, viewed from right side.  
 5. Same, dorsal view.  
 6. Adult male, viewed from left side.

*Cypridopsis monodonta* G. O. Sars.

- Fig. 7. Adult male, viewed from right side.  
 8. Same, dorsal view.  
 9. Posterior corner of left valve, with the dentiform process.

*Cypridopsis serrata* G. O. Sars.

- Fig. 10. Adult female, viewed from right side.  
 11. Same, dorsal view.  
 12. Posterior extremity of shell, showing the peculiar marginal serrations of both valves.

## PLATE LXXI.

*Cypridopsis bidentata* G. O. Sars.

- Fig. 1. Adult female, viewed from right side.  
 2. Same, dorsal view.  
 3. Posterior corner of left valve, with the two dentiform processes.

*Cypridopsis tumidula* G. O. Sars.

- Fig. 4. Adult female, viewed from right side.  
 5. Same, dorsal view.  
 6. Posterior extremity of shell, exhibiting the armature of both valves.

*Cypridopsis congenera* G. O. Sars.

- Fig. 7. Adult female, viewed from right side.  
 8. Same, dorsal view.  
 9. Adult male, viewed from left side.

*Cypridopsis gibba* G. O. Sars.

- Fig. 10. Adult female, viewed from right side.  
 11. Same, dorsal view.  
 12. Adult male, viewed from left side.

## PLATE LXXII.

*Zonocypris costata* Vávra.

- Fig. 1. Adult female, viewed from right side.  
 2. Same, dorsal view.  
 3. Extremity of left inferior antenna, showing the peculiar structure of one of the apical claws.

*Zamocypris laevis* G. O. Sars.

- Fig. 4. Adult female, viewed from right side.  
 5. Same, dorsal view.  
 6. Muscular impressions of right valve.  
 7. Extremity of left inferior antenna.

*Stenocypris perarnata* Brady.

- Fig. 8. Adult female, viewed from right side.  
 9. Same, dorsal view.  
 10. Caudal rami.

*Heterocypris dubia* G. O. Sars.

- Fig. 11. Adult female, viewed from right side.  
 12. Same, dorsal view.  
 13. Muscular impressions of right valve.  
 14. Caudal ramus.

## PLATE LXXIII.

*Ilyocypris propinqua* G. O. Sars.

- Fig. 1. Adult female, viewed from left side.  
 2. Same, dorsal view.  
 3. Muscular impressions of left valve.  
 4. Caudal ramus.

*Ilyocypris alta* G. O. Sars.

- Fig. 5. Adult male, viewed from left side.  
 6. Same, dorsal view.  
 7. Caudal ramus.

*Limnocythere obtusata* G. O. Sars.

- Fig. 8. Adult female, viewed from right side.  
 9. Same, dorsal view.  
 10. Muscular impressions of right valve.  
 11. Superior antenna.  
 12. Inferior antenna.  
 13. Right series of legs.  
 14. Caudal lobe.

*Paracypris curta* G. O. Sars.

- Fig. 15. Adult male, viewed from right side.  
 16. Same, dorsal view.  
 17. Caudal ramus.

6. On *Tritylodon*, and on the Relationships of the  
 Multituberculata. By R. BROOM, M.D., D.Sc., C.M.Z.S.

[Received March 14, 1910.]

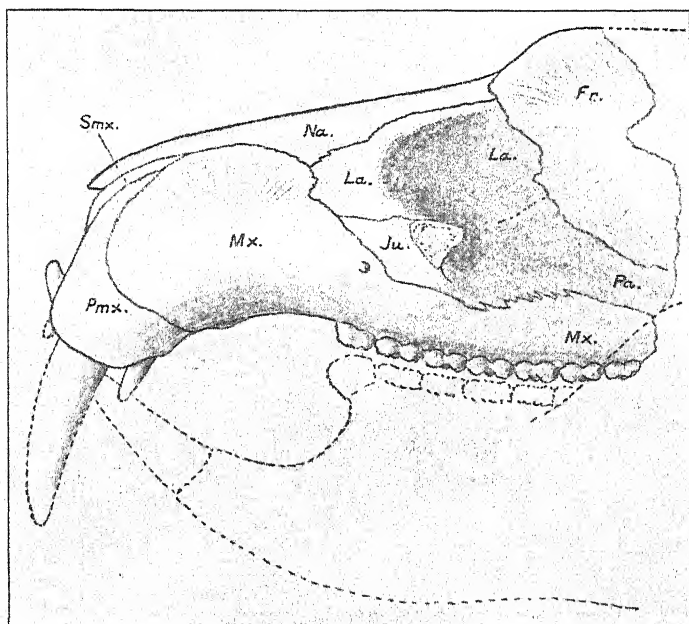
(Text-figures 67 and 68.)

In 1884 Owen described, under the name *Tritylodon longærus*, a very remarkable imperfect skull submitted to him by Dr. Exton, of the Bloemfontein Museum. The specimen was stated to have come from "Thaba-chou, Basutoland," and was believed to be a Triassic mammal allied to the European *Stereognathus*. There is no locality known in Basutoland of the name Thaba-chou, but there are several mountains called Thaba-tsueu, and it is probably from one of these that the specimen came. In any case we now

know that the whole of Basutoland is on beds of Stormberg age; and as the Stormberg beds are situated above the Molteno beds, which are known to be Rhætic, and as they contain remains of true Crocodiles, we may safely assume that they are of Lower Jurassic age, and not Triassic as was supposed.

The specimen, which consists of the almost perfect snout with part of the interorbital region, portions of the malar arch, and the complete palate, was described by Owen at some length, and his figures have been frequently reproduced. Owen's opinion that *Tritylodon* was a mammal was supported by Cope, Osborn, Lydekker, Seeley, and others. In 1894, however, Seeley, as the result of his examination of the Cynodont reptiles, came to the conclusion that *Tritylodon* was really a slightly modified Cynodont reptile: and this view has been followed by a number of later writers.

Text-fig. 67.



Side view of Snout of *Tritylodon longæus* Owen. Nat. size. Slightly restored.

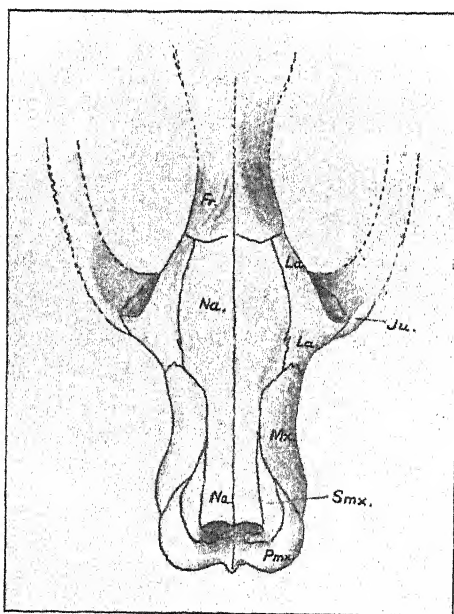
Fr. Frontal. Ju. Jugal. La. Lachrymal. Mx. Maxilla. Na. Nasal.  
Pa. Palatine. Pmx. Premaxilla. Smx. Septomaxilla.

In 1904 I endeavoured to show that none of the arguments advanced by Seeley in favour of *Tritylodon* being a reptile were valid, but that in all points *Tritylodon* was an undoubted mammal.

While recently in London I made a careful study of the type, which, unfortunately, is still the only specimen known, and found that a good deal more could be made out of the original specimen than was supposed.

In a considerable number of points my conclusions differ from those of Owen and Seeley. The flat piece of bone on the upper part of the snout, which both Owen and Seeley believe to be the frontal, I consider without doubt the upper part of the nasal. The pair of imperfect bones, which form a median ridge at the back part of the specimen as preserved, are believed by Owen and Seeley to be the parietals. I regard them as the anterior halves of the frontals. The bone which Seeley believes to be the pre-frontal I hold to be the upper part of the large lachrymal.

Text-fig. 68.



Upper view of snout of *Tritylodon longirostris* Owen.  $\frac{2}{3}$  nat. size.

Fr. Frontal. Ju. Jugal. La. Lachrymal. Ma. Maxilla. Na. Nasal.  
Pmx. Premaxilla. Smx. Septomaxilla.

Owen gives the dental formula as  $i\ 2, m\ 6$ . I believe there are pretty certainly seven molars, and in front of the large incisors there is a socket which probably had a small anterior incisor. I therefore conclude that the formula is  $i\ 3, m\ 7$ . There is undoubted evidence that the lower molars ground with an antero-posterior motion against the upper. The lower incisors most probably passed together between the large upper incisors, which

I believe to be  $i^2$ , and their tips probably rested against the small  $i^1$ .

Between the nasals and the premaxillaries is a pair of well-developed septomaxillaries which have not previously been observed. The position of these bones is seen in the figures given of both side and upper views. The septomaxillary completely separates the premaxillary from the nasal and passes down into the anterior nasal region. There is no evidence that the nares have been separated by a complete internasal process of the premaxillaries.

When the back part of the skull and the lower jaws are restored there is presented a singularly Rodent-like appearance.

As regards the habits of *Tritylodon*, I think it most probable that it was a root-eating animal, the large tusk-like 2nd incisors being well adapted for digging out and breaking off the roots, and the molars with their rows of crescentic tubercles admirably suited for grinding.

*Tritylodon* is the oldest Multituberculate mammal the skull of which is known even partly, and the only other Multituberculate of which much besides the lower jaw is known is one of the latest Eocene types, *Ptilodus*. Fortunately there has recently been discovered and described by Gidley a good skull with the lower jaw in position and a number of the more important bones of the skeleton of *Ptilodus gracilis*.

From the study of *Ptilodus*, Gidley comes to the following very interesting conclusions, which may be stated in his own words:—  
“A fact of first importance is that neither in the skull nor skeleton of the Montana specimen are there any indications of affinities suggesting the Monotremes, while every character is marsupial, as shown in the general arrangement and function of the teeth and the development of the skull and skeleton. The unequal development of the fore and hind limbs, the character of the incisors, the form of the palate, and the position of the cheek-teeth all indicate definite affinities with the Diprotodonts. At the same time the reduction in numbers of the molars and the extreme specialisation of the premolars confirms Osborn's conclusion regarding the phyletic position of the group, namely, that the Multituberculata may be the last representatives of a very ancient phylum that became extinct in the early Tertiary.

“From the foregoing therefore it appears that the Allotheria represent an extinct group of multituberculate Eutherian mammals closely related with but not ancestral to the Diprotodont division of the Marsupialia, with which division they may now be classed as an Infraorder, or Superfamily, their relationship dating back to a common ancestry somewhere in the Jurassic or even to earlier Triassic times, as was suggested by Cope.”

While everyone must be most grateful for the great addition made by Gidley to our knowledge of the Multituberculate structure, I should like to suggest that I think the case is by no

means proven that they are at all closely allied to the Diprotodont Marsupials. There is a little ambiguity in his language where he speaks of "multituberculate *Eutherian* mammals" forming an Infraorder of the Marsupialia. Presumably he means "Metatherian." But it is manifest he regards the Multituberculata as forming a division of the Marsupialia.

Let us consider in some detail the points that are urged in favour of this conclusion.

"Every character," it is said, "is marsupial, as shown in the general arrangement and function of the teeth and the development of the skull and skeleton." If by arrangement is meant the occurrence of incisors, premolars, and molars, without canines, the character is not more marsupial than rodent, and a somewhat similar arrangement is found in the other Eutherian orders. But further the number of the molars seems to me opposed to any close association of the Multituberculates with the Marsupials. No living marsupial has more than three premolars and almost every one has four molars. The Multituberculates have apparently as the normal series four premolars and three molars as in the Eutheria. The whole seven are seen in *Allodon*, and when the number is reduced to six as in *Ptilodus* there seems little doubt that the loss is in front and not behind. From the position of the lower teeth I should incline to the view that the large grooved tooth in *Ptilodus* and the posterior of the grooved teeth in *Plagiular* and *Ctenacodon* are 1st true molars. But whatever difference of opinion may be held on the interpretation of the teeth, there can be little doubt that in structure the molars are quite unlike anything known among Marsupials.

In the structure of the skull the only points bearing on the affinities seem to be the following:—1. "The malar extends backward to the glenoid surface, and apparently joins the lachrymal bone anteriorly as in the living Marsupials." Though the backward extension of the malar is doubtless a marsupial character it is not confined to Marsupials, being found in *Procavia*, *Meritherium*, and other Eutherians. It is a typical character of the Cynodont reptiles and was doubtless present in all early mammals. The meeting of the malar and lachrymal is another Cynodont character which we should expect to find in any early mammal. 2. "The occiput extends but slightly beyond the posterior root of the zygoma." This is a Cynodont character which is not met with in Marsupials\*. Some approach to it is seen in some early Eutherians. 3. "The nasals are relatively large and broad, expanding posteriorly." Still another Cynodont character which is retained by most Marsupials, but also by some Eutherians, e. g. *Hystrix*. 4. "The premaxillaries are short and widely separated from the frontals by the ascending portion of the maxilla." This character is quite common in Eutherians. 5. "The relatively broad, high-arched palate is perforated by two pairs of foramina."

\* But is found in *Ornithorhynchus*.

In Cynodonts the palate is relatively narrow and never perforated. It seems probable that as mastication became established and the palate became greatly widened perforation would be likely to occur. It is still found in most Marsupials, but it is also met with in Eutherians, e. g. *Erinaceus* and *Macroscelides*. 6. "There appears to be an alisphenoid canal and a well-developed alisphenoid bulla." It is admitted that this region is crushed and broken, and that the characters cannot be made out clearly. So far as the figure shows, the condition is very unlike that seen in Marsupials, and the structure of the back of the jaw confirms this. In neither *Ptilodus* nor *Plagiaulax* is there any distinct angle, and in *Ctenacodon* the angle is very small. This is quite unlike what is seen in Marsupials, where both in the Diprotodonts and the Polyprotodonts a well-developed angle curves round a large alisphenoid bulla. 7. "There is a distinct notch on the inferior inner border of the [occipital] condyle, a character also observed in some of the living diprotodont Marsupials." The exact shape of the occipital condyle depends much on the habits of the animal, and most of the marsupial peculiarities seem to be paralleled by some of the higher forms. If we knew the arrangement of the foramina for the ixth, xth, xith, and especially xiith nerves, we would have a point of more value in settling the affinities than anything else connected with the skull. The lower jaw is marsupial in having the lower posterior portion inflected, but in the practical absence of a distinct angle it differs considerably.

The humerus, it is stated, "is distinctly eutherian throughout, and is very unlike that of any of the living Monotremes." Though in general shape it is very unlike the humerus of either *Echidna* or *Ornithorhynchus* and bears a superficial resemblance to that of Marsupials and Eutherians, the lower end is quite unlike anything known in any living mammal, and certainly very different from the ordinary marsupial type. In fact, the articular portion comes nearer to the monotreme type than to that of any of the higher forms.

The pelvis is too imperfect to throw much light on the affinities.

The femur and tibia so far as preserved are certainly not marsupial in type, being very unlike those of either Diprotodonts or Polyprotodonts\*.

Doubtless all the bones both of the skull and limbs are superficially more like those of Marsupials than Monotremes, but one is too apt to forget that the only living Monotremes are degenerate dwarfed digging animals, and are probably much worse types of the Prototheria than *Talpa* and *Chrysochloris* are of the Eutheria.

Taking all the points into consideration, we find that there is nothing in the postcranial skeleton that is distinctly marsupial,

\* The unequal development of the fore and hind limbs is a point of no weight in determining affinities. The condition in *Macropus* is probably a very recent modification. A similar development is met with in hopping animals of various orders, e. g. *Macroscelides*, *Pedetes*, &c.



and in the skull only the inflexion of the jaw and the palatal vacuities. All the other supposed marsupial characters are primitive features probably present in all early mammals.

On the other hand, there are one or two characters strongly opposed to any association of the Multituberculata with Marsupials. (1) While there is no evidence of any reduction in the number of molars, there are never more than three (or according to Gidley two). In *Tritylodon* we seem to have the full set of four premolars and three molars. In *Ctenacodon*, *Plagiailax*, and *Ptilodus* we get a progressive reduction of the premolars but the molars remain constant. Further, the multituberculate condition is quite unlike anything known in Marsupials. It may have been an evolution from ordinary tritubercular molars, but if *Triglyphus* is really Triassic then the Multituberculates appeared much before the earliest-known trituberculate types and may possibly have been independently evolved from a prototherian ancestor. (2) The presence of a well-developed septomaxillary in *Tritylodon* suggests affinity with the Monotremes and is opposed to a close relationship with the Marsupials. Both *Echidna* and *Ornithorhynchus*, as shown by Gaupp, have large septomaxillaries. No marsupial is known to have a septomaxillary, though a small one appears to occur in *Dasypus*, as I have shown. (3) The far backward position of the glenoid cavity is also against a marsupial affinity and in favour of the Multituberculates being a more primitive type.

In Upper Triassic time we have numerous Cynodont reptiles, some so like mammals that it is often difficult to be sure whether they are mammals or not. We also have the earliest-known supposed mammals, represented by jaws with very primitive teeth. These earliest mammals can hardly have been other than Prototherians, and as the Multituberculates also appear to arise in the Triassic and *Tritylodon* is certainly not later than Lower Jurassic, it seems most likely that they are an offshoot from the early Prototherian group. The Multituberculates can be traced right on to Eocene times and form a well-marked group with no close affinities to any other later mammals. The Marsupials of to-day are apparently a lately evolved group which sprang from a diphyodont placental ancestor probably in Cretaceous times. A *Didelphys*-like form is perhaps the most primitive type, and from it have been derived the various Polyprotodont types, including *Cenolestes*, which for many reasons I have long looked upon as a slightly modified Polyprotodont, and later on in Australia have been evolved the Diprotodonts.

If we are right in concluding that the Diprotodont marsupials originated in Australia in Tertiary times from a Polyprotodont ancestor which was itself derived in later Mesozoic times from a diphyodont placental, it is difficult to believe that the Multituberculates which originated in Triassic times can be in any way nearly related to them. In the present state of our knowledge it seems wisest to leave the Multituberculata as a distinct

independent group with no very near affinities with the living Monotremes, Marsupials, or Eutherians.

About fifty years ago there was much discussion between Owen and Falconer and others as to the habits of *Plagiaulax*, Owen holding that it was a carnivore, the others that it was a vegetarian. Since then everyone who has expressed any opinion on the subject has sided with Falconer; and Gidley is also opposed to Owen. He says:—"The evidence that *Ptilodus* and *Plagiaulax* were not carnivorous in habits seems rather conclusive, but as to whether they were insectivorous, herbivorous, or frugivorous there may still be some differences of opinion. I am inclined to consider them as frugivorous since the incisors were well fitted for picking small fruits or berries, while the large cutting blades of the lower premolars were admirably adapted to cutting or slicing the rinds of tough-skinned berries, or to chopping up fleshy fruits held against the blunt-pointed premolars of the upper jaw. For masticating the seeds of such small fruits and berries the multituberculate molars were amply sufficient."

It has long seemed to me that as with *Thylacoleo* so with *Plagiaulax*, Owen was right in regarding it as a carnivore. The large size of the temporal fossæ for the accommodation of powerful temporal muscles, the small extent of the grinding surface, the cutting mechanism of the anterior molars or premolars, and the pointed condition and the mode of implanting of the incisors together with their mode of passing between the upper incisors, all seem to me to favour a carnivorous habit. An insectivorous habit, however, seems not improbable, and most small Carnivores are also partly insectivorous. But a herbivorous habit for such forms as *Plagiaulax* or *Ptilodus* seems to me very improbable, and a frugivorous habit well-nigh impossible. *Ptilodus* from the great disparity of its limbs must have been a ground-hopping animal which was probably quite unable to climb trees. Even if it could, fruits and berries are only ripe at one or two seasons of the year, and an animal can only be a satisfactory frugivorous form if it can fly from place to place like the frugivorous bats or birds. Further, typical frugivorous forms like *Pteropus* seem to require neither powerful long incisors nor large cutting molars or premolars. But the most serious objection to *Plagiaulax* being a frugivorous form is the fact that *Plagiaulax* lived in Jurassic times, whereas what evidence there is, is against flowering plants having been on the earth before Lower Cretaceous times. Conifers, Cycads, and Ginkgoes occurred before the Cretaceous, but, so far as we know, no fruits or berries in the ordinary sense.

It may be urged that the carnivorous mechanism of *Plagiaulax* is of a different type from that of modern carnivorous mammals, but there is this important point to bear in mind. Present-day Carnivores almost exclusively feed on other mammals or birds or in some cases fish. But the carnivorous mammals of Mesozoic times had to feed probably almost exclusively on reptiles. With the exception of *Tritylodon*, which was probably a root-eating

animal, it is doubtful if we know of any other herbivorous type of mammal in Jurassic times. The long-jawed many-toothed small forms were probably insectivorous, the short-jawed Multituberculates for the most part carnivorous. The peculiar cutting premolars and molars of the latter probably were used for cutting the scaly skins of lizards, and the tubercular molars for crushing the bones. Possibly in Eocene times they became extinct owing to the development of the Creodonts, a better carnivorous type.

*Literature referred to.*

- R. OWEN.—“On the Skull and Dentition of a Triassic Mammal (*Tritylodon longærus* Owen) from South Africa.” Q. J. G. S. vol. xl. 1884, p. 146.
- H. G. SEELEY.—“The Reputed Mammals from the Karroo Formation of Cape Colony.” Phil. Trans. 1895, p. 1025.
- R. BROOM.—“On the Affinities of *Tritylodon*.” Tr. S. Afr. Phil. Soc. vol. xvi. pt. 1, 1905, p. 73.
- J. W. GIDLEY.—“Notes on the Fossil Mammalian Genus *Ptilodus*, with Descriptions of new Species.” Proc. U.S. Nat. Mus. vol. xxxvi. No. 1689, 1909, p. 611.

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May 24, 1910.

DR. HENRY WOODWARD, F.R.S., Vice-President,  
in the Chair.

The Secretary read the following report on the additions made to the Society's Menagerie during the month of April, 1910:—

The number of registered additions to the Society's Menagerie during the month of April last was 249. Of these 148 were acquired by presentation, 52 by purchase, 26 were received on deposit, 9 in exchange, and 14 were born in the Gardens.

The number of departures during the same period, by deaths and removals, was 158.

Amongst the additions special attention may be directed to:—

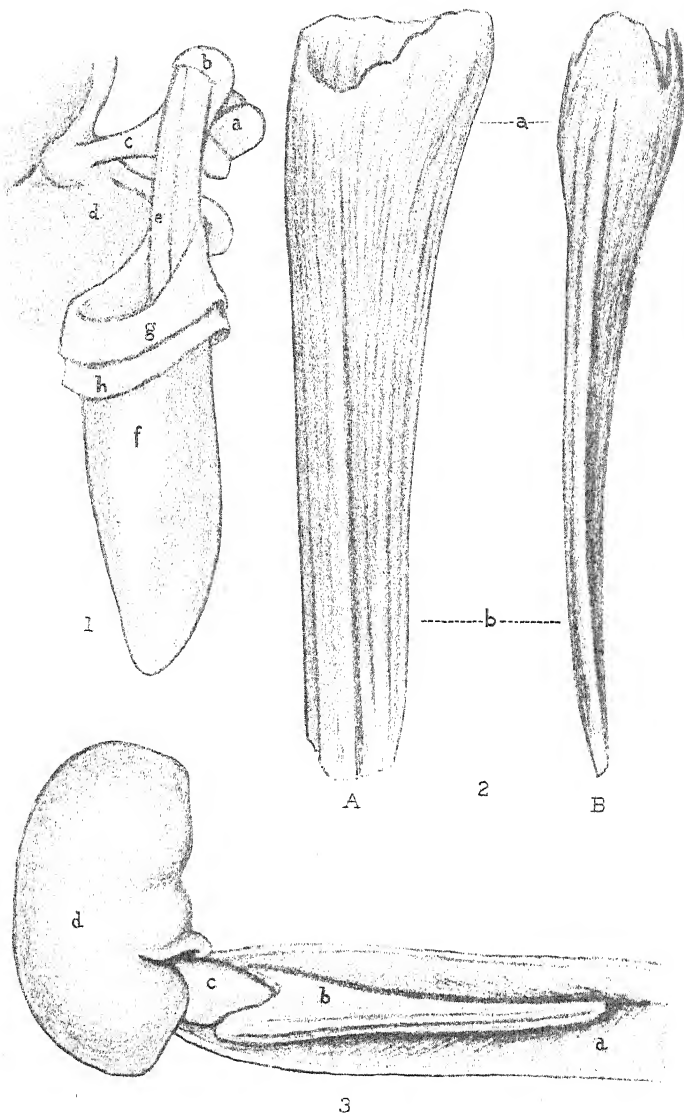
1 Lar Gibbon (*Hylobates lar*), from Siam, presented on April 13th by Lt. Stephen St. L. Moore, R.N.

1 Tayra (*Galera barbara*) and 1 Kinkajou (*Cercoleptes caudivolvulus*), from Manãos, presented on April 14th by E. Salis Schwabe, Esq., C.M.Z.S.

1 Monk-Seal (*Monachus albiventer*), from Madeira, presented on April 9th by Godfrey Williams, Esq., F.Z.S.

1 Bay Duiker (*Cephalophus dorsalis*), 1 Zech's Mole-Rat (*Georychus zechi*), new to the Collection, and 1 Beautiful Wood-Hawk (*Dryotriorchis spectabilis*), from Obuassi, S. Ashanti, presented on April 1st by Capt. C. H. Armitage.





Bale & Danielsson, Ltd

AUDITORY APPARATUS OF BALÆNOPTERA MUSCULUS.

1 Tasmanian Wolf (*Thylacinus cynocephalus*), from Tasmania, purchased on April 18th.

2 Bearded Vultures (*Gypaëtus barbatus*), from Europe, purchased on April 9th.

4 Mortier's Water-Hens (*Tribonyx mortieri*), from Tasmania, purchased on April 18th.

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Mr. Ernest Gibson, F.Z.S., exhibited a skin of *Felis geoffroyi* and made some remarks on the distribution of the animal.

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The following papers were read :—

1. Observations on the Anatomy and General Biology of some Members of the Larger Cetacea. By D. G. LILLIE, B.A., Hutchinson Research Student of St. John's College, Cambridge\*.

[Received March 16, 1910.]

(Plate LXXIV.† and Text-figures 69-78)

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- I. Introduction.
- II. The Species captured at Innishkea.
- III. The Occurrence of Hairs in Whales.
- IV. The Auditory Organ of *Balaenoptera*.
- V. The Asymmetry of the Odontocete Skull.
- VI. Notes on the Species :—
  - (1) *Balaenoptera musculus* Linnaeus.
  - (2) *Balaenoptera sibbaldii* Gray.
  - (3) *Physeter macrocephalus* Linnaeus.
- VII. Miscellaneous Observations :—
  - (1) Locality of Captures.
  - (2) Diving Powers.
  - (3) Copulation, Period of Gestation, and Rate of Breeding.

#### I. INTRODUCTION.

Within the past seven years six whaling stations have been established in various outlying parts of the British Isles. Four stations have been opened on the mainland of Shetland, one in North Harris in the Hebrides‡, and one on the island of South Innishkea in the west of Ireland. Mr. R. C. Haldane §, of

\* Communicated by Dr. HANS GADOW, F.R.S., F.Z.S.

† For explanation of the Plate see p. 792.

‡ For an admirable short account of the history of whaling and of its recent establishment in Scotland, see two papers by the late Thomas Southwell: *Annals of Scottish Nat. Hist.* 1904, vol. xiii, p. 77; and *Annals & Magazine of Nat. Hist.* ser. 7, vol. xvi, 1905. See also Lillie, *Proc. Cambridge Phil. Soc.* vol. xv, pt. iv, p. 347.

§ R. C. Haldane, *Annals of Scottish Nat. Hist.* 1904-1909.

Lochend, Shetland, availing himself of the opportunities thus offered, has collected and published much information relating to the larger Cetacea captured in Scottish waters since the opening of these whaling stations.

Hitherto, our knowledge of whales has been chiefly derived from isolated specimens stranded from time to time in various localities around the coasts of civilised countries. Some of these, though often in an advanced state of decay, have been examined by zoologists, and a few observations have been added to the large though scattered Cetacean literature. The fact that the whaling industry has been confined to the wildest regions of the earth and carried on under the severest conditions of physical privation has prevented other than chance observations of this nature being made.

The establishment of whaling stations near our shores should give a new impetus to the study of Cetology and induce competent observers to visit the stations during the whaling seasons. It may be hoped that new light will be thrown upon the many obscure problems in the biology of whales before these much hunted animals become too scarce.

During the spring of 1908 a whaling station was opened in the west of Ireland, by the Aranmore Whaling Company, on the island of South Innishkea off the coast of Co. Mayo; and a certain gentleman, who wishes to remain anonymous, prompted by considerations such as the above, came forward with a sum of money for the encouragement of the study of the Irish Cetacea. This fund, which was added to by others, was placed in the hands of Dr. S. F. Harmer, F.R.S., Keeper of Zoology in the British Museum (Natural History), who was asked to find someone to visit the Irish station for as long a period as possible during the summer of 1909 for the purpose of studying the anatomy, the specific characters, the general biology, and other questions of scientific interest relating to the larger Cetacea. I had the good fortune to be chosen for the work, and accordingly went to Innishkea on the 6th of July 1909 and remained there until the 26th of August, a period of seven weeks.

This visit took place about the middle of the whaling season, which begins early in May and continues up to the end of September. The capture of whales last year was very intermittent and depended largely on the weather. During the first part of my stay at Innishkea the weather was unusually rough for July and only one whale was caught in four weeks, while in the last fortnight I saw nearly thirty whales brought to shore.

The huge size of the animals makes any examination of them very difficult, even at a whaling station with all the necessary appliances for their dissection at hand. The length of the specimens seen at Innishkea varied between the limits of 50 and 80 feet in a straight line. Any whale under 40 feet is, according to the whalers, not worth shooting. The whalers have a definite method of cutting up a whale which no doubt is best suited to their purpose, though from the point of view of the anatomist the

process leaves much to be desired. The latter has to make the best of the operations however, and it is so essential in the whaling trade to dispose of the whales as rapidly as possible, while the oil is fresh, that the whalers can hardly be expected to study the needs of the anatomist. A whole animal 70 feet in length will often disappear completely in the course of a morning.

When a number of whales are brought in at the same time, as is often the case, the zoologist is not greatly benefited, for they are all anchored to buoys at some little distance from the shore, and brought to the "flensing slip" one by one to be stripped of their whalebone and blubber. The carcasses are then taken back to the buoy to wait until they can be further dealt with. This method of procedure is rendered necessary on account of there being no room for more than three or four whales on the "flensing slip" at the same time.

The whales are artificially inflated with air directly they are killed, and they are then easily towed home by the whaling steamer. This inflation is often a source of great inconvenience to the anatomist, since portions of the viscera are torn away and shot out of the body-cavity when the body-wall is pierced by the flensing knife.

Enough has been said to show that to the scientific man a whaling station does not pretend to offer the advantages of unlimited time and comfort which are to be found in a laboratory. But at a station all the largest whales, with the exception of *Bulena mysticetus* and *Rhachianectes glaucus*, can usually be seen within the space of three months. Very frequently several individuals of different species can be examined and compared as regards their external and internal characters. The material is often sufficiently fresh for histological study, which, on account of the gigantic size of the animals, should prove of considerable interest. Moreover, exceptional opportunities are offered to the naturalist of going out to sea in the whaling steamers. Many interesting observations upon the habits of the Cetacea could possibly be made by this means alone.

With regard to the smaller Cetaceans, since they are seldom killed by man at present, material is difficult to obtain; but the study of these animals is not at the moment so pressing as that of the rapidly decreasing larger forms.

Before passing to consider the observations resulting from my stay of seven weeks at Innishkea I wish to express my thanks to the anonymous donors who made the visit possible, and to many friends who have helped me to carry out the work.

My special thanks are due to Dr. S. F. Harmer, F.R.S., who has kindly read the proof-sheets, for entrusting me with the research and for his valuable help and advice. I would also express my hearty thanks to Mr. R. M. Barrington, F.L.S., for his kindness in many ways and for giving me the benefit of his local knowledge. I am under obligations to the Rev. W. S. Green, C.B., Chief Inspector of Fisheries for Ireland,



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and to Mr. E. W. L. Holt for much kindness shown to me at Innishkea. I cannot express my thanks too warmly for the cordial help and hospitality accorded to me by Captain Arff-Pettersen, Mr. E. Christensen, and others at the Whaling Station. My sincere thanks are due to Mr. A. E. Shipley, F.R.S., for many kindnesses. To Dr. W. T. Calman I am indebted for the determination of the Crustacea. Finally, to Dr. H. Gadow, F.R.S., I am very deeply grateful for his valuable help with regard to several anatomical points.

## II. THE SPECIES CAPTURED AT INNISHKEA.

The catch of whales at Innishkea for the opening season of 1908 numbered 77, and was as follows \* :—

- 5 *Balæna biscayensis* Gray.
- 21 *Balænoptera musculus* Linnaeus.
- 19 *Balænoptera sibbaldii* Gray.
- 31 *Balænoptera borealis* Lesson.
- 1 *Megaptera longimana* Rudolphi.

The total number of whales caught during the season of 1909 was 102. These consisted of five species. The numbers and average length of the individuals are given in the following table :—

Species.	Total number killed.	Number of Bulls.	Average length of Bulls.	Number of Cows.	Average length of Cows.
<i>Balæna biscayensis</i> Gray .....	5	4	ft. ins. 43 6	1	ft. ins. 43 0
<i>Balænoptera musculus</i> Linnaeus.	56	27	58 3	29	60 0
<i>Balænoptera sibbaldii</i> Gray ...	27	13	65 5	14	66 5
<i>Balænoptera borealis</i> Lesson ...	9	4	43 0	5	42 0
<i>Physeter macrocephalus</i> Linnaeus	5	5	55 7	...	...

Thus the list of species taken off Innishkea is as follows :—

- Balæna biscayensis* Gray,
- Balænoptera musculus* Linnaeus,
- Balænoptera sibbaldii* Gray,
- Balænoptera borealis* Lesson,
- Megaptera longimana* Rudolphi,
- Physeter macrocephalus* Linnaeus,

\* Haldane, Annals of Scottish Nat. Hist. April 1909, p. 68.

and includes all the largest known species of whales with the exception of *Balæna mysticetus* Linnæus and *Rhachianectes glaucus* Cope. Several smaller Cetaceans are seen off the west coast of Ireland, but they are not killed by the whalers. These include *Balenoptera rostrata* Gray, and some members of the subfamily Ziphiinæ and the family Delphiinidæ.

The specimens of *Balæna biscayensis* Gray, killed last summer, were taken during the first fortnight of June. This species is said by the whalers to leave our shores after the end of June. *Balenoptera musculus* Linnæus was equally plentiful from the beginning of May till the end of the season. *Balenoptera sibbaldii* Gray was taken from the end of June till September. The captures of *Balenoptera borealis* Lesson, were restricted to the last half of May and the first half of June, the last specimen being caught ten days before the first *B. sibbaldii* Gray was taken. This whale is said to leave our shores upon the arrival of *B. sibbaldii*. The Sperm Whales (*Physeter macrocephalus* Linnæus) were captured between the middle of June and the end of July. If detailed records of the captures of whales continue to be kept for the Irish stations \* to compare with those published by Mr. Haldane for the Scotch stations, we may hope, by this means, to throw some light upon the migrations of these creatures.

During my stay at Innishkea the following whales were captured: 21 specimens of *Balenoptera musculus* Linnæus, 15 of which were examined; 20 individuals of *B. sibbaldii* Gray, 15 of which were examined; and two male Sperm Whales (*Physeter macrocephalus* Linnæus), both of which were examined. The results obtained from the examination of these whales will now be described.

### III. THE OCCURRENCE OF HAIRS IN WHALES.

The distribution and significance of the scanty hairs of the Cetacea do not appear to have been hitherto studied in the detail they deserve. They have been vaguely referred to as occurring on the jaws of some adult forms †. Sometimes they have been found on the foetus only.

In two adult Sperm Whales (*Physeter macrocephalus* Linnæus) seen at Innishkea, no trace of hairs could be found on any part of the animals even after careful searching.

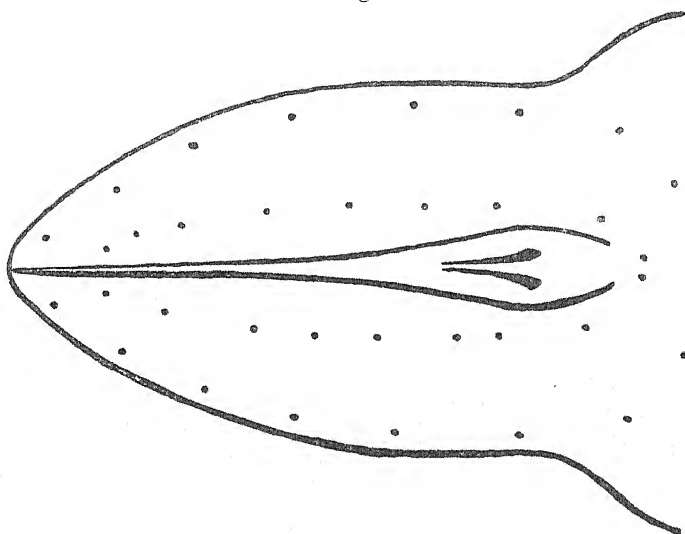
In the case, however, of the Rorquals *Balenoptera musculus* Linnæus, and *B. sibbaldii* Gray, some 15 individuals of each species were examined, and it was found that a definite distribution of hairs could be made out in each case. Four rows of straight, white, bristle-like hairs from half an inch to an inch in length occur on the dorsal surface of the back or facial region of

\* A second Irish station is expected to be opened for the season 1910.

† Knox, Proc. Roy. Soc. Edinb. i. 1833-4. Eschricht & Reinhardt, "Om Nord-hvalen," Copenhagen, 1861. Collett, Proc. Zool. Soc. 1886, p. 255. Cunningham, Proc. Zool. Soc. 1876, p. 680. Clark, Proc. Zool. Soc. 1876, p. 688.

the head (see text-fig. 69). These consist of two inner rows on either side of the median ridge which bears the blow-holes or external nares, and two outer rows following the edges of the beak from points just behind the blow-holes to its anterior extremity. The average number of hairs in each row is about eight. The hairs in each row occur at irregular intervals, but they always keep to the above-mentioned lines of distribution whether there are more or less than eight hairs forming a row.

Text-fig. 69.

Dorsal surface of the beak of *Balanoptera sibbaldii* Gray, showing hairs.

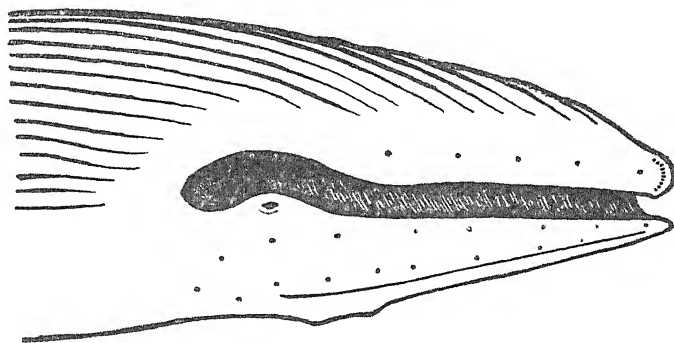
On each side of the lower jaw (text-fig. 70) there was a row of some five or more hairs running from the tip of the mandible along the middle line of the outer edge of each ramus to a point just in front of the eye. At the extreme anterior end of the mandible (see text-fig. 70), over the ligamentous junction of the rami, there were also two vertical rows of hairs set at right angles to those last mentioned. These occur close together and run parallel to each other from the upper to the under surface of each ramus. The hairs in these two rows are placed closer together than in the others, there being generally about fourteen hairs in each row.

The relations of the hairs to the epidermis and adjoining layers in *Balanoptera musculus* Linnæus, have been figured and described by G. O. Sars\* in a paper published in 1865; but further work requires to be done in order to determine whether they possess a tactile function or not.

\* Sars, Vidensk.-Selskabets Forhandlinger for 1865.

On looking through the Cetacean literature there appears to be no record of the occurrence of hairs in adult Odontocetes. It would seem that the presence of hairs in the adult is restricted to the Whalebone Whales; and their retention and distribution over the beak and mandible in these forms may be due to their possessing a tactile function and thus serve to indicate to the animal the presence of its food. The small size of the Crustacea which generally form the food of the Mystacoceti make them difficult to see, and since the olfactory organs of the Cetacea are very reduced, the occurrence of tactile hairs over the oral region may be an advantage, as the small food-animals might brush against them and thus inform the whale when to open its mouth.

Text-fig. 70.



Lateral view of the head of *Balanoptera sibbaldii* Gray, to show the hairs.

The top of the snout of a whale is, of course, only the prolonged upper lip, where one would naturally look for vibrissæ. In one of the figures given by Sars in the paper above mentioned, what appears to be a nerve is seen traversing the blubber at the base of the hair; which would point to a tactile function. On this theory, the food of the Odontocetes being of a larger size the presence of tactile hairs is not so obviously required, and hence the hairy covering has entirely vanished in the adult forms of these whales.

On the other hand it is also conceivable that the vibrissæ, because of their relative stoutness, should be the last hairs to disappear; and the fact that they have reached a further stage of degeneration in the Odontocetes than they have in the Whalebone Whales may be purely accidental.

#### IV. THE AUDITORY ORGAN OF *BALANOPTERA*.

The auditory apparatus in several individuals of *Balanoptera musculus* and *B. sibbaldii* was examined with some difficulty. The parts of the ear agreed fairly well in both these species with

those parts of the auditory organ, in *Balenoptera rostrata*, which were described by Drs. Carte and Macalister\* in their excellent paper on the anatomy of a member of that species published in 1867. Dr. Dwight† has also described the bones of the auditory organ of *B. musculus* at some length in a paper published in 1872. It will thus be only necessary briefly to recapitulate here the parts of the organ which are already known and to add some observations which appear to be new.

The opening of the external auditory meatus on the surface of the head is a relatively small slit situated at a short distance behind the eye in a horizontal line with the commissure of the lips. There is no trace of a pinna. The auditory canal is continued backwards from this aperture until it reaches as far as the zygomatic process of the squamosal bone where it turns inwards and, increasing somewhat in diameter, proceeds along a groove in the squamosal bone (text-fig. 71, *Sg.*<sup>1</sup>) which winds round the posterior border of that bone to reach the tympanic membrane. The diameter of this tube towards its inner and wider extremity was about one and a half inches in the two species under consideration.

The tympanic membrane (Pl. LXXIV. fig. 1) seems to have escaped the notice of previous observers. It is highly modified and is a sac-like structure not unlike the finger of a glove. The sac (Pl. LXXIV. fig. 1, *f*) is about three inches long and three-quarters of an inch in diameter and tapers to a rounded point at the outer or distal end. The walls of the sac are about one-tenth of an inch in thickness, and consist chiefly of white fibrous tissue and yellow elastic tissue. No nerve-cells or fibres and no muscle-fibres have been found up to the present. From the upper surface of the sac in the median line a ligament about an inch long and 5 mm. in diameter projects forwards towards the tympanic cavity. The ligament is continued along the sac in the opposite direction as a ridge. The total length of the tympanic sac and ligament is about four inches. The mouth of the sac opens into the tympanic cavity, while the outer portion projects into the external auditory meatus. The inner extremity of the latter joins the rim of the sac (Pl. LXXIV. fig. 1, *h*). The ligamentous process passes under the junction of the malleus and incus, and becomes attached at its proximal end to the very much reduced manubrium of the malleus. The malleus is fused to the tympanic bone, as has been already pointed out by Drs. Carte and Macalister. Thus in *Balenoptera* the tympanic membrane has become a sac-like organ, which projects outwards and is attached by a ligament to a rigid process of the tympanic bone—this process being the malleus.

In the external auditory meatus of all the individuals examined at Innishkea there was a solid plug of wax-like substance of fairly definite size and shape which does not seem to have been hitherto described. This plug (Pl. LXXIV. fig. 2) was usually about

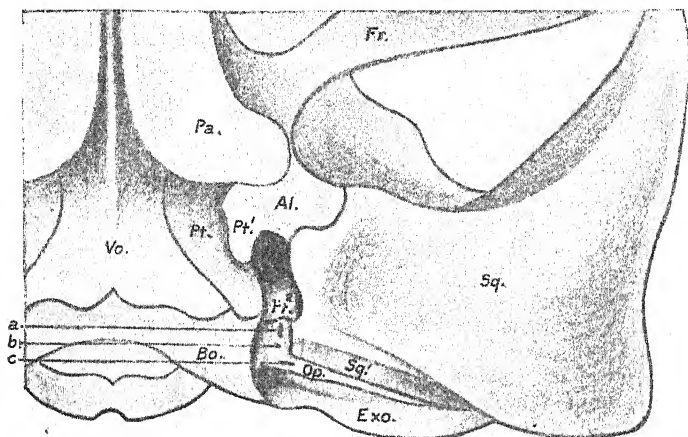
\* Carte & Macalister, Phil. Trans. 1867, p. 252.

† Dwight, Memoirs Boston Soc. Nat. Hist. 1872, vol. ii. p. 225.

5 inches long and  $1\frac{1}{2}$  inches broad at the wider end. It consisted of a deposit of ear-wax, which formed a coat to the outer surface of the tympanic membrane in that region where the latter projected into the external auditory meatus. The deposit formed a solid mass, which could easily be detached from the tympanic membrane. The inner portion of the plug had the form of an oval cup (Pl. LXXIV. fig. 2, *a*), measuring about  $1\frac{1}{2}$  inches across the broadest part and approximately 1 inch deep. The outer portion, however, formed a solid thin flattened rod about 4 inches long and 1 inch broad (Pl. LXXIV. fig. 2, *b*). The auditory canal appeared to be full of water, in which the tympanic membrane was immersed, with the attached plug of wax lying in a horizontal position. The total length of the membrane and plug thus projecting into the auditory canal was about 6 inches (Pl. LXXIV. fig. 3).

The Cetacea have a remarkable depression on the base of the cranium on each side of the median line (text-fig. 71).

Text-fig. 71.



Ventral view of left posterior portion of the skull of *Balenoptera musculus* Linnaeus  
The tympanic bone has been removed.

*Fr.* = Frontal; *Pa.* = Palatine; *Vo.* = Vomer; *Al.* = Alisphenoid; *Pt.* = Pterygoid; *Pt.*<sup>1</sup> = Pterygoid plate of alisphenoid; *Pt.*<sup>2</sup> = Portion of pterygoid, forming roof of pterygoid fossa; *Sq.* = Zygomatic process of squamosal; *Sq.*<sup>1</sup> = Zygomatic process of squamosal, forming roof of groove in which lies the inner portion of the external auditory meatus with the plug of ear-wax; *a.*, anterior pedicle for attachment of tympanic bone, situated on pro-otic portion of periotic; *b.*, fenestra ovalis, situated on the labyrinthine segment of periotic; *c.*, posterior pedicle of tympanic bone, situated on opisthotic portion of periotic; *Op.*, opisthotic portion of periotic; *Bo.*, basioccipital; *Exo.*, exoccipital.

In *Balenoptera* these depressions are bounded posteriorly by the projecting edge of the exoccipital, externally by the base of the zygomatic process of the squamosal, on the inner side behind by



the prominent edge of the basioccipital. The anterior portion of the inner side of this depression and the front of the recess are bounded by the pterygoid and alisphenoid bones, which are fused together; the latter also form the roof of the anterior half of the depression. Thus the anterior portion of the cavity is bounded on three sides by the pterygoid and externally by the squamosal, and is known as the pterygoid fossa.

In this recess the united tympanic and periotic\* bones lie. The latter consists of three parts: an anterior or pro-otic, a central or labyrinthic, and a posterior or opisthotic. The anterior or pro-otic bone resembles a three-sided pyramid with its apex pointing forwards and projecting into a cavity in the squamosal bone above the roof of the pterygoid fossa.

On the inferior surface of the pro-otic, at its posterior end, there is a longitudinally flattened pedicle which unites with the anterior extremity of the tympanic bone. Just behind this anterior pedicle of the tympanic—that is, between the pro-otic portion and the central or labyrinthic—there is a groove running in a transverse direction. This furrow forms the roof of the auditory meatus. The central or labyrinthic portion is the smallest of the three divisions of the periotic, and it contains the vestibule, the cochlea, and the diminutive semicircular canals. The inferior surface of this bone is dome-shaped and forms the roof of the tympanic cavity. The fenestra ovalis is situated in the depression which marks the outer border of this bone on the under side. The fenestra rotunda is placed some little distance behind the fenestra ovalis, and is separated from the latter by a ridge which forms the posterior boundary of the tympanic cavity above. The fenestra rotunda is thus on the posterior surface of the labyrinthic segment, and thus outside the tympanic cavity. The superior surface of the labyrinthic bone is irregular in shape and is turned towards the cranial cavity. Two foramina open on this surface—the aqueductus Fallopii anteriorly and the internal auditory meatus posteriorly. The aqueductus perforates the bone and opens at the base of the labyrinthic segment, and is continuous with a groove in the opisthotic division. At the posterior end of the labyrinthic the opisthotic segment extends outwards; it is constricted at its origin, but broadens and expands towards its extremity between the squamosal and exoccipital bones almost at right angles to the pro-otic portion. In fact, the labyrinthic may be said to lie at the angle formed by the pro-otic and opisthotic. The tympanic segment is united to the ends of these two bones by pedicles, which are flattened in the direction of their length. Thus the posterior pedicle is situated on the inferior surface of the opisthotic, near its junction with the labyrinthic, and is at right angles to the anterior pedicle.

The tympanic bone† (Pl. LXXIV. fig. 3, *d*), which is attached to the periotic as described above, is usually about five inches long

\* Carte & Macalister, Phil. Trans. 1867, pl. vi. fig. 11.

† Carte & Macalister, *loc. cit.* pl. vi. fig. 10; pl. vii. fig. 6.

and shaped like a cowrie shell. It occupies the posterior half of the depression, into which it fits fairly closely (text-fig. 71, *a, c*), its outer inferior surface being level with the projecting edge of the basioccipital, the pterygoid fossa lying immediately in front. The tympanic bone may be said to have an inner and an outer surface, which meet below. The inner surface is flat, its lower edge lying near, but not touching, that of the projecting process of the basioccipital; its upper edge is smooth and rolled into the cavity of the bone. The outer side of the tympanic is rounded, with the convexity pointing outwards. The upper edge of this outer side forms an irregular extended lip, which gives rise to the anterior and posterior pedicles. On this lip, immediately behind the anterior pedicle and at right angles to it, there is a ridge projecting upwards and nearly touching the periotic. The inner edge of this ridge is continuous with the processus longus of the malleus, the malleus thus being fused to the tympanic bone. This process, which runs parallel to the posterior pedicle, together with the latter, form the sides of the auditory meatus.

The malleus has been described by Drs. Carte and Macalister\*, and is stated by these authors to be fused to the tympanic bone by the handle or manubrium; whereas Dr. Dwight† regards that portion of the malleus which has co-ossified with the bulla as the processus longus or gracilis. The latter would seem to be the correct interpretation judging from the mode of attachment of the tympanic membrane. This structure was apparently lost or had decayed in the specimens dissected by the above-mentioned writers, so they could only guess at the relationship of the parts. The manubrium is reduced to a short process, slightly hooked at its distal end (Pl. LXXIV. fig. 1, *b*), on the ventral surface of which is attached the ligament of the tympanic membrane. This is the only attachment of the membrane to the malleus. The rim of the tympanic membrane sac is joined to the inner extremity of the external auditory canal. The processus longus or gracilis (Pl. LXXIV. fig. 1, *c*) is well developed, and is fused to the inner edge of the lip of the tympanic bulla. The incus and stapes have been described by previous writers‡, and are morphologically similar to those found in other Mammals.

At the anterior end of the tympanic cavity, in front of the anterior pedicle of the tympanic bone, there is an opening which communicates with the pterygoid fossa. This may be regarded as the enlarged inner end of the Eustachian tube. The pterygoid fossa, which measures from 6 to 8 inches in length, about 4 inches in width, and 4 inches in depth, is also a portion of the Eustachian tube, for it is lined by the same mucous membrane as the tympanic cavity and the Eustachian tube proper. The latter is a relatively narrow canal, about three-quarters of an inch in diameter, which opens out of the floor of the pterygoid fossa and winds along a

\* Carte & Macalister, *loc. cit.* p. 254.

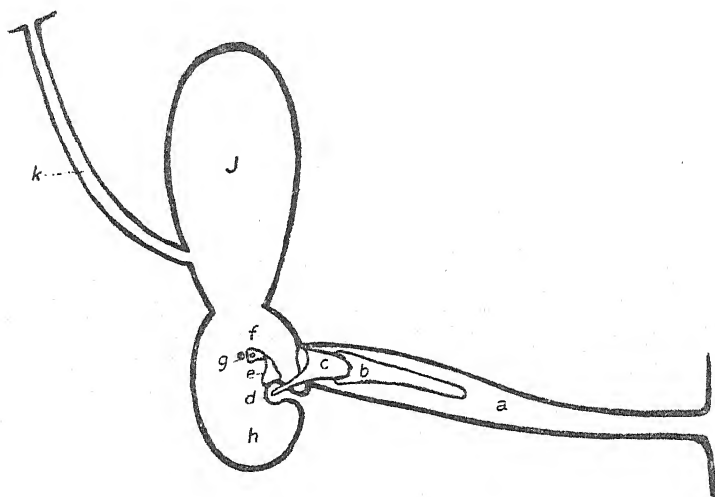
† Dwight, Mem. Boston Soc. Nat. Hist. 1872, vol. ii. p. 226.

‡ Carte & Macalister, *loc. cit.* p. 254; Dwight, *loc. cit.* p. 226.

groove on the inner side of the pterygoid plate of the alisphenoid (text-fig. 71, Pt.<sup>1</sup>, p. 777) to open into the alveolated nasopharyngeal chamber near the junction of the nares. This tube is about one foot in length in the larger specimens. The mucous membrane, which lines the Eustachian tube and is continued into the pterygoid fossa and tympanic cavity, lies directly on the bony walls of these cavities and covers over the ossicles.

The cavities of the middle ear are probably filled with air through the Eustachian tube (text-fig. 72), while the external ear appears to be filled with water. The pressure of the water upon the tympanic membrane when the whale dives must be considerable, and it is

Text-fig. 72.

Diagrammatic view of the outer and middle ear of *Balanoptera*.

*a*=external auditory meatus; *l*=plug of ear-wax; *c*=tympanic membrane attached to malleus by ligament; *d*=malleus fused to tympanic bone; *e*=incus; *f*=stapes; *g*=fenestra ovalis; *h*=tympanic cavity; *J*=pterygoid fossa; *k*=Eustachian tube.

curious that the membrane should be concave on its inner side instead of on the outer side. The sac-like membrane, being connected by a ligament to the rigid malleus, cannot have a vibrating function. The animal probably fills the middle ear with air on coming to the surface to breathe. When the creature dives, this air is imprisoned by the closing of the Eustachian tube. The walls of the latter are provided with a strong sphincter muscle. The air in the Eustachian tube would be forced into the pterygoid fossa and tympanic cavity when the tube was compressed, and would inflate the sac-like tympanic membrane. This air would be approximately at atmospheric pressure. The increase of pressure

produced by the water on the external surface of the membrane as the animal dived would tend to compress the walls of the sac. There may be some means by which this increased pressure is made known to the animal, and thus enable the curiously modified tympanic membrane to serve as a pressure-gauge; but it is not possible to assign any function to the structure at present.

The whale probably receives sound-vibrations by means of vibrating bony surfaces, after the manner of fishes. The tympanic bulla is a relatively dense and heavy sounding-box, fastened to the petrotic bone by two thin pedicles, so that it could be easily set in vibration. The bulla is connected with the fenestra ovalis by the chain of ossicles, the auditory apparatus being thus independent of the tympanic membrane, which may have some other function, possibly that of a pressure-gauge.

The description of the ear of *Balaena mysticetus* given by Home\* in 1823 seems to correspond to some extent with the above account of that organ in *Balenoptera*. The ear of the *Odontocetes* appears to be more like that of ordinary Mammals †.

#### V. THE ASYMMETRY OF THE ODONTOCETE SKULL.

It has long been recognized that a want of symmetry exists in the Odontocete skull, centred round the nasal region; but authorities seem still to be at a loss to account for this irregularity. Mr. Beddard‡ sums up the difficulty thus:—"It is easier to say that the asymmetry, being, as it is, chiefly developed in the regions of the blow-holes, has something to do with these structures, than to find any adequate reason for connecting the two." From an examination of the skull alone an explanation certainly does not present itself very readily. But when the anatomy of the head and neck of a symmetrical Mysticocete, such as *Balenoptera musculus* Linnaeus, is examined, and the relations of all the parts studied and compared with those of an asymmetrical Odontocete, such as *Physeter macrocephalus* Linnaeus, the problem becomes greatly simplified, and a solution seems to offer itself.

In the Cetacea the arytenoid and epiglottidean cartilages form a long, rigid, cylindrical tube, a continuation of the larynx, which rises up through the floor of the pharynx like a pillar and is thrust up between the alveolated walls of the nasopharyngeal chamber, which form the roof of the pharynx in this region. In the larger whales this pipe is about one foot in length. A somewhat similar pipe-like epiglottis, connecting the larynx with the posterior nares also occurs in the Marsupials and Ungulates; but it is less pronounced than in the Cetacea.

In the case of the symmetrical Mysticocetes this tube is

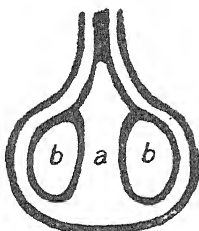
\* Home, 'Lectures on Comparative Anatomy' (1823), Vol. iii. Lect. IX., Vol. iv. Tab. c. & ci.

† Hunter, Phil. Trans. 1787, p. 430.

‡ Beddard, 'A Book of Whales', p. 49.

situated in the middle of the pharynx. The food of these whales, consisting as it does of small Crustaceans, can readily enter the comparatively narrow pharynx and find a passage down the pharynx on each side of the pipe (see text-fig. 73).

Text-fig. 73.

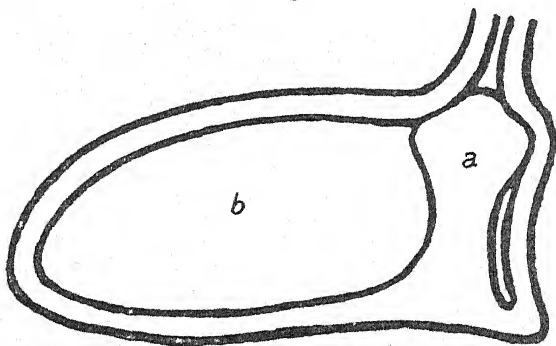


Transverse section (diagrammatic) of the pharynx of a Mysticocete.

*a* = epiglottis; *b* = food-passage.

In the Odontocete *Physeter* the pharynx is fully four or five times as large as that of a *Balaenoptera* of the same length, and the pipe-like epiglottis, instead of being placed in the middle of the pharynx, is on the left side close against the left wall of the latter. The pipe passes up into the nasopharyngeal chamber, which has alveolated walls; as in *Balaenoptera*, this

Text-fig. 74.

Transverse section (diagrammatic) of the pharynx of *Physeter*.

*a* = epiglottis; *b* = food-passage.

chamber communicates with the posterior nares situated on the left side of the skull. The comparatively large animals eaten by this whale, which are always swallowed whole, pass down the spacious pharynx only on the right side of the pipe, which is close up against the left wall and leaves plenty of room for their transit (see text-fig. 74). Thus the pharynx of *Physeter* in the region of

the glottis is divided into a right half for the passage of food and a left half for respiration. This arrangement gives an asymmetrical form to the nasal regions of the skull.

Pouchet and Beauregard\*, in their admirable memoir on the anatomy of the Sperm Whale, refer to the pipe-like epiglottis as being asymmetrically placed; but they state that it was situated on the right side of the pharynx, whereas in both the specimens of *Physeter* seen at Innishkea the pipe was undoubtedly on the left side. These authors appear to have attached no significance to the position of the epiglottis as bearing upon the asymmetry of the skull.

## VI. NOTES ON THE SPECIES.

### 1. *BALÆNOPTERA MUSCULUS* Linnaeus †.

The length, form, and proportions of all the specimens seen were in accordance with previous descriptions of the species.

*Colour.* There appeared to be two colour-types in this species, distinguished by the colour of the dorsal surface. In the more common type the colour of the dorsal surface was bluish black; in the other variety the dorsal surface was brownish black, almost sepia. This fact has been noticed by Mr. Haldane‡, who attributes the difference in colour to a light-effect; but it was sufficiently marked in all the individuals landed during my visit for them to be placed in either one or other of the two groups.

The asymmetrical colouring of the face was remarkably constant in all the specimens. On the right side the outer edge of the beak was white or light grey; on the left side the beak was entirely bluish black or sepia in colour, according to the variety which the individual belonged to. The anterior third of the baleen plates on the right side were invariably white, the remainder on that side being dark grey or black on the outer halves of the plates and becoming lighter in colour towards their inner edges. On the left side all the baleen plates were similar to the posterior plates of the right side. The bristles were invariably white all round the mouth, and not black as stated by Mr. Collett§ in his synopsis of the four northern species of *Balænoptera*. The lower jaw was white on the right side, and bluish black or sepia on the left side. The whole underside of the body, the right lower jaw, the inner side of the paddles, and the under side of the flukes of the tail were white in all cases. The roof of the mouth consists of a broad oval margin of white bristles surrounding a narrow strip of pink palate, and below, a pink tongue covered with dark grey mottling. Every specimen had whitish oblong spots distributed over the dark parts of the body, identical, except in

\* Pouchet et Beauregard, *Nouvelles Archives du Muséum (Paris)*, 3 sér. vol. iv 1892, p. 59, pl. iii.

† Known also as *B. physalus* Fabricius, *B. rorqual* Lacépède, *Physalus antiquorum* Gray.

‡ Haldane, *Annals of Scottish Nat. Hist.* 1908, p. 70.

§ Collett, *Proc. Zool. Soc.* 1886, p. 265.

size, with those figured and described by Mr. Collett\* as occurring in *B. borealis*. The spots in *B. musculus* usually did not exceed 50 mm. in length.

*Throat-grooves*.—In several individuals of both *B. musculus* and *B. sibbaldii* the skin lining the grooves in the throat-region had a bright red appearance. It unfortunately did not occur to me at the time to ascertain the cause of this; but I am inclined to think that the red colour of the grooves may be due to their being very highly vascular, and thus helping to aerate the blood. The throat-grooves of *Balaenoptera* occupy about half of the ventral surface of the body, extending from the anterior end of the mandible to the navel. In *B. musculus* there are about 100 of these grooves, in the other species about 60. The skin lining the furrows is extremely elastic. When unextended the grooves are about an inch in width; when extended they are often six inches wide. Thus they would give a large aerating surface. Undoubtedly the principal function of these elastic furrows on the throat is to increase the size of the mouth-cavity, so that a large volume of water containing Crustaceans can be taken in at each mouthful. The water is strained off through the whalebone plates, and afterwards the food is swallowed. In *Balaena* the mouth itself is very large, owing to the arched form of the skull, so that its capacity is naturally ample. Hence the absence of throat-grooves in the Right Whales. The function of the grooves as an aerating surface or external gill, if it occurs at all, would be a secondary one. This theory, however, would enable us to understand the extraordinary powers of remaining under water attributed to *Balaenoptera* which will be referred to later in this paper.

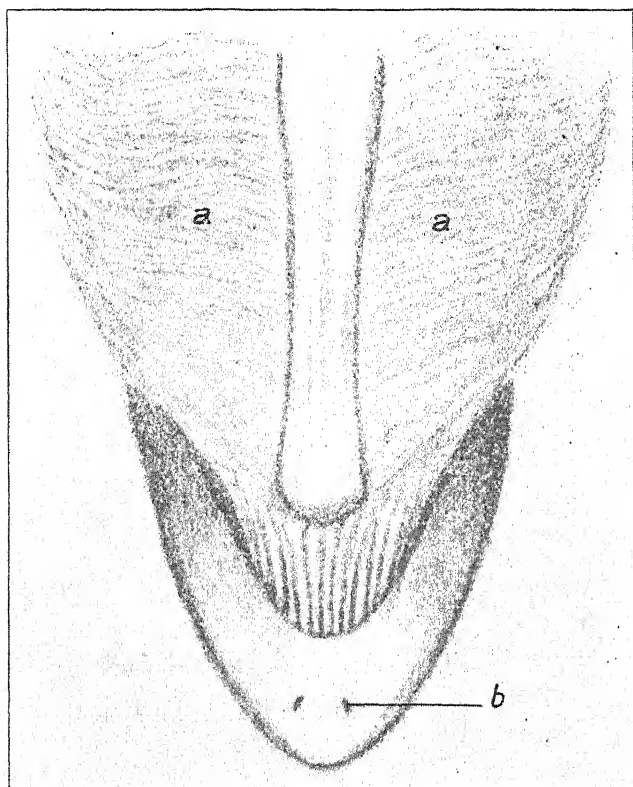
*Jacobson's organ*.—On the under surface of the snout, about half way between its extreme tip and the small anterior filaments of whalebone, there were two small apertures leading into narrow tubes which ended blindly about two inches from their mouths (text-fig. 75). These were the ducts of the organ of Jacobson. In *B. sibbaldii* they are only represented by two small depressions. In most Mammals these organs communicate with the nostrils, but in an adult *B. musculus* they are separated from the nostrils by a distance of some ten feet, and are interesting examples of the persistence of traces of an organ after it has become obsolete. It is just possible that the small ducts in *B. musculus* may have some function, but they were not equally well developed in all the individuals examined, and in one specimen they were reduced to mere depressions very much like those of *B. sibbaldii*.

*Testes*.—In a member of this species, 51 feet long, the testes were measured and found to be only 9 inches in length and 3 inches in diameter. In a specimen 60 feet long the testes were 2 feet 6 inches in length and nearly a foot in diameter. This shows that male members of this species reach maturity when between 50 and 60 feet long.

\* Proc. Zool. Soc. 1886, p. 249, pl. xxvi. fig. 2.

*Penis*.—In the Cetacea the penis when not in use is capable of being entirely withdrawn into the body-cavity. The ventral surface of the body is thus left free from any protuberance which would hinder the animal in swimming. The testes remain permanently inside the body-cavity. The penis of an adult *B. musculus* measures from 5 to 6 feet in length when fully extended; it is about a foot in diameter at the base, tapering to a relatively fine point.

Text-fig. 75.



Ventral view of anterior extremity of the beak of *Balanoptera musculus* Linnaeus  
*a* = hairy inner surface of baleen plates; *b* = external openings of the organ.  
Jacobson.

*Food*.—An examination was made of the stomach-contents of nearly all the specimens of this species caught during the months of July and August, and it was found that only one individual, killed on July 13th, had fed upon herrings. The alimentary



canals of all the others contained *Meganyctiphanes norregica* M. Sars (formerly called *Nyctiphanes norregica*). Other species of Euphausiidae may have been present but only the above mentioned was definitely determined. In the pharynx these Crustaceans were found practically intact; in the stomach they were more broken up, and in the intestines they were reduced to a thick terra-cotta coloured fluid, the red colour being due to a red pigment commonly found in the Euphausiidae.

*Fetuses*.—On July 31st, 1909, two female *B. musculus* were killed, one was 63 feet long and contained a fetus 1 foot in length. The other was 67 feet long and contained a fetus 5½ feet in length. This tends to support the view that the species under consideration and possibly other species of *Balenoptera* have no definite breeding season.

*Parasites*.—The external surfaces of all the *B. musculus* examined were entirely free from parasites with the exception of the baleen plates. These were very frequently coated with the adult forms and nauplius larvæ of *Balenophilus unisetus* Auvillius. These remarkable Copepods have been found on the baleen plates of *B. borealis* and *B. sibbaldii*\*, but this appears to be the first record of their occurrence on *B. musculus*.

## 2. *BALENOPTERA SIBBALDII* Gray (*B. latirostris* Flower).

The external characters of all the Innishkea specimens were in agreement with the descriptions of the species given by previous observers.

The inside of the mouth, the baleen, bristles, palate and tongue were entirely black.

The forms of the paddles and dorsal fins of *B. sibbaldii* differ from those of *B. musculus*, as is shown by the diagrams (text-figs. 76 & 77). It would seem that the presence of a dorsal fin is restricted to the fast-swimming Cetaceans.

The contents of the alimentary canals were examined in the case of some ten individuals of this species, caught during August, and found to consist exclusively of *Meganyctiphanes norregica* in all cases.

A young male member of this species, 63 feet long, was killed while following the mother and feeding upon her milk. The specimen had Crustaceans in its stomach, showing that it did not depend entirely upon the mother for food. The young of *B. sibbaldii* are said to be between 20 and 30 feet in length at birth, so, unless the period of lactation is unusually prolonged, this would point to a comparatively rapid growth and development in the larger Cetacea as is maintained by Mr. Haldane†. If the period of lactation continued, as is generally supposed, for one year the animal would increase in size to the extent of over 30 feet in its first year of life.

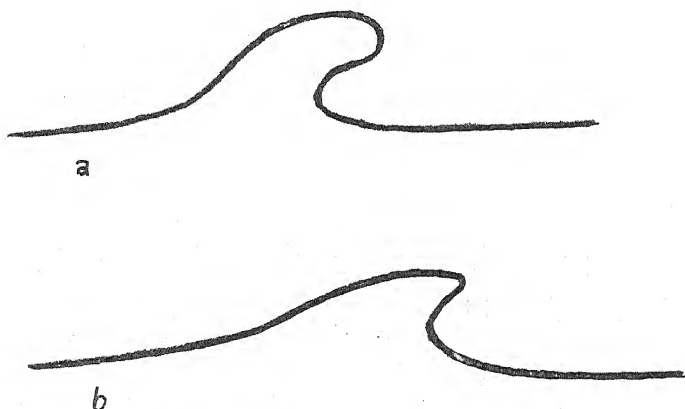
The external surfaces of all the individuals of this species were

\* Collett, Proc. Zool. Soc. 1886, p. 243.

† Haldane, Annals of Scottish Nat. Hist. April 1905, p. 69.

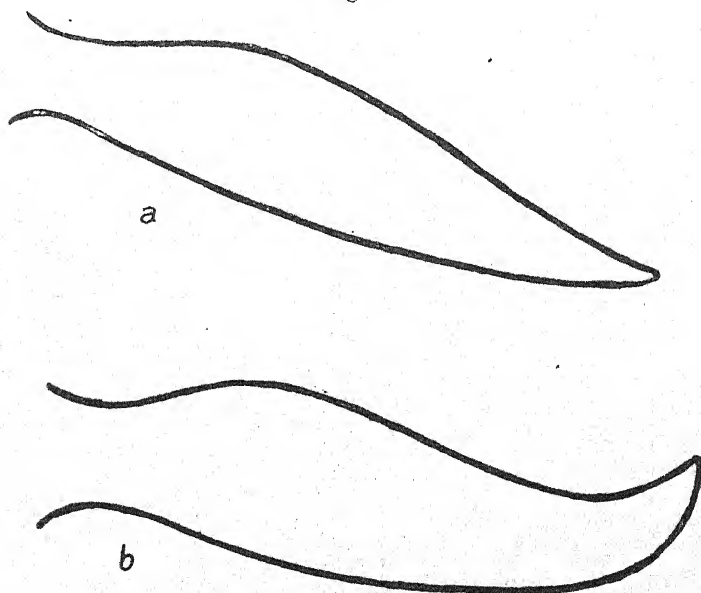
remarkably free from parasites, the only species found being *Balenophilus unisetus* Aurivillius on the baleen plates. No internal parasites could be found.

Text-fig. 76.



dorsal fins of *a. Balenoptera musculus* Linnaeus; *b. Balenoptera sibbaldii* Gray.

Text-fig. 77.



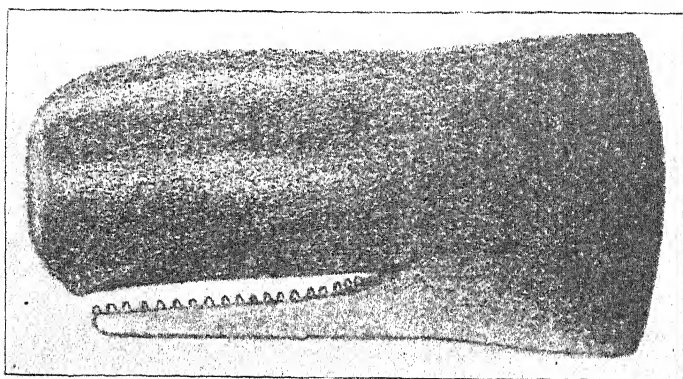
Paddles of *a. Balenoptera musculus* Linnaeus; *b. Balenoptera sibbaldii* Gray.

3. *PHYSETER MACROCEPHALUS* Linnaeus\*.

Two male Sperm Whales were captured during my visit. Their general appearance corresponded with the descriptions of previous observers. But, as there seems to be a little uncertainty concerning the shape of the head of this whale, a sketch is given (text-fig. 78) of the form of the head in the Innishkea specimens.

The upper part of the animal was black, the ventral surface and lower jaw a light bluish grey. A white oval patch occurred in the middle of the ventral surface, extending from a point just in front of the navel to the anus.

Text-fig. 78.

View of the left side of the head of *Physeter macrocephalus* Linnaeus.

On the surface of the head of one of the specimens, on the left side immediately over the position of the nasal bone of the skull, there was a small groove-like depression about two inches deep and five inches long. This slit was placed longitudinally and in a straight line with the blow-hole. It may possibly have been a vestige of an old nasal opening which was situated further back than the present position of the blow-hole.

One of these whales had 24 teeth on each side of the lower jaw. Six of those on the right and eight on the left side were broken. No sign of teeth could be found in the upper jaw.

The alimentary canals of the two Sperm Whales contained the remains of cuttlefish, and the marks of their horny denticulate suckers could be seen all over the surface of the lower jaw and extending more than half-way up the head of each whale, from its anterior extremity to the paddles. The marks of the suckers varied from faintly dotted circular imprints, formed by the slight

\* Probably synonymous with *P. catodon* Fabricius; *P. gibbosus* Schreber; *P. trumpo* Gerard; *P. polyclystus* Couch; *Catodon australis* MacLeay; *C. colneti* Gray; *P. polycephalus* Quoy and Gaimard.

impress of the horny teeth of the suckers upon the epidermis, to deep circular cuts reaching to the blubber. In many cases the epidermis had peeled off from within the deeply cut circles, exposing the corium. The circles varied in diameter from  $\frac{1}{4}$  inch or less to  $1\frac{1}{2}$  inches according to the size of the sucker which formed them. These marks were noticed by Pouchet and Beaugerard\* as occurring on the head of a Sperm Whale and were attributed by them to parasitic Cirripedes which had become detached. But, after comparing these marks with the horny rings of the suckers taken from the stomachs and intestines of the two specimens, and taking into account the fact that the marks only occur on the head, there can be no doubt that they were made by cuttlefish during their struggles with the Sperm Whales who had seized them for food. The marking of the skin of *Odontocetes* by cuttlefish has been referred to by Dr. Harmer†.

A group of barnacles was found attached to the fourth anterior tooth on the right side of the lower jaw of one of these whales. The cluster consisted of individuals of *Conchoderma auritum*, to one of which was attached a small specimen of *C. virgatum*. These were the only external parasites to be seen on the two Sperm Whales.

The guts of both specimens were infested with internal parasites. The determination of these is in progress.

Several of the whales were fresh enough to have permitted an examination to be made of their histology and of their gut Protozoa; but unfortunately the necessary apparatus for such work was not at hand at Innishkea. This was to be regretted since the gut Protozoa of the Cetacea are quite unknown and very little, if anything, has been written upon the histology of whales.

## VII. MISCELLANEOUS OBSERVATIONS.

### 1. *Locality of Captures.*

When the station at Innishkea was first opened in the early summer of 1908, whales were taken at a distance of ten miles from the island. But during the season of 1909 the steamers had to go at least sixty miles out to sea before they could find a whale. It was not possible to obtain the exact latitude and longitude of the captures, as these were kept as trade secrets by the whalers. However, it is safe to say that all the whales obtained by this station during the two seasons of its existence were taken within a radius of seventy miles, north, south and west of Innishkea. This can be explained either by their being molested or by an alteration in the distribution of their food.

During my visit one of the whaling captains discovered about twenty individuals of *Balenoptera musculus* occupying the head

\* Pouchet et Beaugerard, Nouvelles Archives du Muséum (Paris), 3 sér. vol. i. 1889, p. 9.

† Harmer, Trans. Norfolk and Norwich Naturalists' Soc. vol. vii. 1901, p. 185.

of an inlet or bay about sixty miles north-west of Innishkea within the 1000 fathom contour. He hunted this spot for three weeks, always finding the whales there, and was still doing so when I left. I took an opportunity of visiting the place with him about the middle of August and was impressed with the apparent regularity in the habits of the animals. Between daybreak and 10 A.M. they were to be seen swimming in this deep inlet and blowing every ten minutes. After 10 A.M. they disappeared for the rest of the day, but were all back again in the same place the next morning. The captain always appeared on the ground at daybreak, killed one or two and towed them home during the day, returning to the locality over night.

It is maintained by the whalers that the *Balenoptera* spend several hours near the surface each day blowing every ten minutes and storing their blood and lungs with air, and that they then go down and remain below for perhaps eight or twelve hours at a time. They are said to avoid the heat of the day by remaining under water during that period and appearing at the surface in the early morning and evening. On dull cold days they may be at the surface at any time during the day, though they are most plentiful at sunrise. Mr. Collett\* appears to have been given the same account by whalers. The explanation of these habits attributed to the *Balenoptera*, if they really occur, may be the rising and sinking of the plankton eaten by the Crustaceans which form the staple food of these whales. It is more likely that the mid-day heat may have some effect on the plankton, and thus affect the whales indirectly, than that there should be any direct influence.

## 2. Diving Powers.

I made enquiries of the whalers on this subject and I was told that whales, when struck by the harpoon, often dive to the bottom and sometimes come up with stones adhering to the ventral surface. This, however, has been denied by other whalers. During my visit I found on the under surface of one of the specimens of *B. musculus* landed at Innishkea a few broken spines of Echinoderms, which had pierced the epidermis and were lying between it and the corium. A harpooned whale is said to have come to the surface with stones attached to its under surface when killed at a locality where the depth was given as 100 fathoms on the chart. If a naturalist were to spend sufficient time on board a whaling steamer he could probably settle this point, for the whales, when dead, always turn over on their backs and float with the ventral surface uppermost, so there would be no difficulty in detecting any adhering stones if they were present. Assuming that a harpooned whale does not act very differently as regards diving powers to one under normal conditions, this would be a simple method of ascertaining what those powers are. Of course

\* Collett, Proc. Zool. Soc. 1886, p. 263.

the objection will be raised that if stones are found on the under surface, how is one to make sure how long they have been there? On this point I was assured by my informant that the stones are generally so lightly attached that they soon fall off, and a whale could not travel far with them. If we may assume that this is correct, when a whale is captured with stones on the ventral surface it is only necessary to ascertain the depth of the sea at the locality of capture, by referring to the chart, to ascertain the depth to which the creature has dived on being harpooned. It is said by the whalers that when a harpooned whale, after breaking the harpoon-rope, dives to a depth of 60 fathoms and dies, it comes to the surface at the end of three days; whereas if it goes below this depth and dies it never reappears. There seemed to be unanimous agreement among the whalers upon this point.

### 3. *Copulation, Period of Gestation and Rate of Breeding.*

The *Balaenoptera* are said by whalers to copulate at the surface of the sea. The pair swim towards each other and turn slightly on their sides so that their ventral surfaces face one another. The male makes several dashes at the female to insert the penis. When the pair first rush together the long axes of their bodies are parallel with the surface of the sea; but they curve up vertically at the end of the act. After copulation the male is said to be exhausted and easily caught.

As regards the period of gestation and the rate of breeding among Cetaceans, it is difficult to see how any definite information can be obtained on these and similar subjects, which are of interest to the cetologist and of considerable importance commercially, unless individuals are kept in a confined place for purposes of observation. This would perhaps not be such an impossible undertaking as it would at first appear. Of the many deep sounds or straits, through which the tides pass, on the western coasts of Ireland and Scotland, one could doubtless be found which could be converted into an aquarium for whales. To do this it would only be necessary to place barriers at the mouths of the strait in order to imprison the animal and yet allow of the ingress and egress of the tide and food-supply. The animals would have to be caught by the Japanese method of capturing whales, which consists of throwing a large rope-net over the animal and towing it to the shore alive. *Balaena biscayensis* Gray, has been taken by this method and possibly other species also\*.

A Whalebone Whale imprisoned in a strait could probably be kept alive on the organisms swept in by each tide.

Until some such scheme as this is brought to pass we must continue to remain in ignorance, or be content with vague speculations, concerning many points in the biology of the larger Cetacea.

\* K. Möbius, Sitzungsberichte der Akademie der Wissenschaften zu Berlin, lii. 1893.

## EXPLANATION OF PLATE LXXIV.

Fig. 1. Posterior view of the right tympanic membrane of *Balanoptera musculus* Linnaeus, showing its attachment to the malleus.

- a. Head of malleus with the two articular surfaces for the incus.
- b. Manubrium of malleus.
- c. Processus longus of malleus.
- d. Portion of the lip of the tympanic bone to which the processus longus of the malleus is fused.
- e. Ligament of tympanic membrane.
- f. Sac-like tympanic membrane.
- g. Portion of the mucous membrane lining the tympanic cavity.
- h. Wall of external auditory canal which has been cut near its junction with the rim of the tympanic membrane-sac.

Fig. 2. Plug of ear-wax from the external auditory meatus of *Balanoptera musculus* Linnaeus. A. Dorsal view of plug. B. Posterior view.

- a. Cup-like portion for the reception of the tympanic membrane.
- b. Flattened distal portion.

Fig. 3. Ventral view of the left tympanic bone and inner portion of the external auditory meatus of *Balanoptera musculus* Linnaeus.

- a. Inner portion of external auditory meatus with the ventral wall removed to show the tympanic membrane and plug.
- b. Plug of ear-wax.
- c. Tympanic membrane.
- d. Tympanic bone.

## 2. Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunningham, F.Z.S., 1904-1905.—Report on the Rotifera. By CHARLES F. ROUSSELET, F.R.M.S.\*

[Received April 7, 1910.]

(Plate LXXV.†)

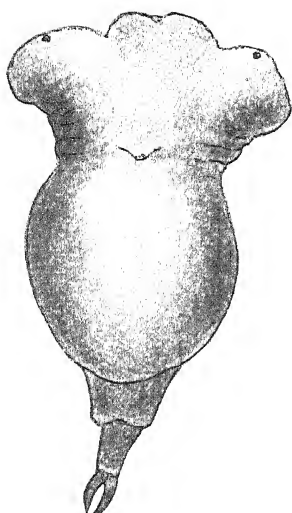
Amongst the collections brought back by Dr. W. A. Cunningham from the great inland lakes of Central Africa, visited during this Expedition, were a number of tubes containing fine surface Plankton nettings which I have searched over for Rotifera.

The gatherings were not specially made with a view to collect these creatures, and being, moreover, made only from a boat in the open water and never among the vegetation near the shore, these circumstances may account for the comparatively poor results obtained.

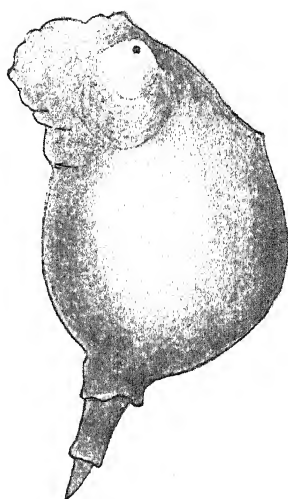
The Collection is, however, interesting and important from the fact that, with the exception of 8 species (excluding doubtful ones) collected in and near the Victoria Nyanza by Dr. Stuhlmann in 1891 and described by Dr. Ant. Collin (1) in 1896, and 14 additional species (again excluding the doubtful ones) collected in the Victoria Nyanza by Dr. Borgert in 1904, and described by Prof. E. von Daday (2) in 1907, no previous records of Rotifera

\* Communicated by Dr. W. A. CUNNINGTON, F.Z.S.

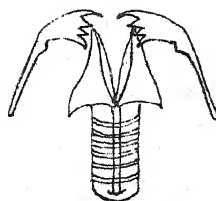
† For explanation of the Plate see p. 799.



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F.R.DIXON-NUTTALL, del. ad. NAT.

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NOTOPS LOFUANA ROUSSELET.





from the Central African Region, and particularly from Lakes Tanganyika and Nyasa, have been made.

The tubes examined by me came from three lakes :—

1. Lake Tanganyika, including the Lofu river.
2. Lake Nyasa.
3. Victoria Nyanza.

From these I obtained a total number of 37 species, of which 11 had already been recorded from the Victoria Nyanza and adjacent region. Most of these species have a wide distribution and are known from various parts of the world, and only one species, from the Lofu river, can be described as new.

In order to make this record of Central African Rotifera complete, I will preface my results with the list of species found by the above mentioned authors, Dr. Collin and Prof. v. Daday, in and about Victoria Nyanza, excluding the doubtful species not identified :—

- Rotifer vulgaris* Ehrenbg. (C.)  
*Philodina emini* Collin. (C.)  
*Triarthra longiseta* Ehrenbg. (D.)  
*Asplanchna brightwelli* Gosse. (D.)  
*Notops macrourus* Barr. & Dad. (D.)  
*Copeus copeus* Ehrenbg. (C.)  
*Tetramastix opoliensis* Zach. (D.)  
*Euchlanis longicaudata* Collin. (C.)  
 (Which is identical with *Euchlanis propatula* Gosse.)  
*Monostyla bulla* Gosse. (D.)  
*Notens stuhlmanni* Collin. (C.)  
*Brachionus rubens* Ehrenbg. (C.; D.)  
 „ *angularis* Gosse. (D.)  
 „ *bakeri* Ehrenbg. (D.)  
 „ *forficula* Wierz. (D.)  
 „ *fulcatus* Zach. (D.)  
 „ *pala* Ehrenbg. (D.)  
 „ *militaris* Ehrenbg. (D.)  
 „ *tetracanthus* Collin = *B. caudatus* Barr. & Dad.  
 (C.; D.)  
*Schizocerca diversicornis* var. *homoceros* Daday. (D.)  
*Anuraea aculeata* Ehrenbg. (D.)  
 „ „ var. *valga* Ehrenbg. (C.)  
 „ *cochlearis* Gosse. (D.)  
*Pedalion mirum* Hudson. (D.)

#### LAKE TANGANYIKA.

From this lake a large number of tubes were available, collected from October 1904 to February 1905, all fine tow-nettings made some distance from the shore and near the following localities :— Mbete, southern end of lake ; Komba Bay, south-western corner ; Kala, a short distance up the eastern shore ; Kasawa, on the west

coast; Vua harbour, on the west coast; Bismarburg (Kasanga), on the east coast; Maswa, on the east coast.

All these samples contained vast quantities of microscopic algae and diatoms; but though I searched most diligently for many days and weeks, I succeeded in finding only 10 species of Rotifera, and very few specimens of these, and nothing new. This paucity of Rotatorian life is certainly most remarkable for such a vast lake; but it is probable that, had collections been made amongst the vegetation near the shore, a greater number and variety might have been obtained. I understand that the water of this lake was formerly somewhat brackish, though the actual salinity was never ascertained, and also that the Cladocera are totally absent, whilst the Copepods are abundant.

*Rotifera found in Lake Tanganyika.*

*Oecistes* (sp. ?) (tubes only, on *Plumatella*).

*Polyarthra platyptera* Ehrenbg.

*Synchorda* (sp. ?) (badly preserved and wholly contracted).

*Asplanchna intermedia* Hudson.

*Rattulus stylatus* Gosse.

*Cathypna lena* Ehrenbg.

*Monostyla bulla* Gosse.

*Salpina brevispina* Ehrenbg.

*Anuraea aculeata* Ehrenbg.

*Brachionus pala* Ehrenbg. (very small variety).

Of these, the only species which was found in some abundance and from various parts of the lake is the small variety of *Brachionus pala*, measuring only  $205\ \mu$  in total length of the lorica. The European specimens usually measure  $325\ \mu$ , and some exceptionally large specimens found in Ormsby Broad, in Norfolk, attain a size of  $442\ \mu$ .

Special interest attaches to the presence in Tanganyika of *Asplanchna intermedia*, as I was not able to record any member of this genus from South Africa (3).

LOFU RIVER.

The Lofu river is a large tributary of Lake Tanganyika, entering it at its extreme south-western corner. I give a separate list of species found in this river, as the Rotatorian fauna shows a marked increase in numbers and variety as compared with those found in the lake.

Although only two small tubes of material were collected by the tow-net, I obtained therefrom 23 species, one of which is new to science and altogether different from anything known; the specimen is figured on Plate LXXV. and described below under the name of *Notops lofuana*, sp. n. The two gatherings were made in October 1904 about a mile and a half from the mouth of the river, so that it is quite clear that a far greater number of

Rotifers are carried into the lake by this river than can afterwards be found in its water.

*Rotifera found in the Lofu River.*

- Ecistes mucicola* Kellicott.  
*Limnias* (sp. ?) (tubes only).  
*Callidina* (sp. ?) (wholly contracted).  
*Synchata oblonga* Ehrenbg.  
*Notops lofuana*, sp. n., Rousselet.  
*Proales daphnicola* Thompson.  
*Rattulus longiseta* Schrank.  
 „ *gracilis* Tessin.  
 „ *bicristatus* Gosse.  
 „ *macerus* Gosse.  
*Euchlanis hyalina* Hudson.  
 „ *oropha* Gosse.  
 „ *propatula* Gosse.  
*Monostyla lunaris* Ehrenbg.  
*Cathypna leontina* Turner.  
 „ *ungulata* Gosse.  
 „ *luna* Ehrenbg.  
*Salpina macracantha* Gosse.  
*Pterodina trilobata* Shephard.  
*Noteus quadricornis* Ehrenbg.  
 „ „ var. *brevispinus* Daday.  
*Brachionus militaris* Ehrenbg.  
*Anuraea aculeata* var. *valga* Ehrenbg.

NOTOPS LOFUANA, sp. n. (Plate LXXV. figs. 1-3.)

Amongst the Rotifera found in the Lofu river there is one new species which appears so different from any known kind, that I find difficulty in assigning it to any known genus. Unfortunately the only specimen available is not sufficiently well preserved to enable one to be sure that the integument is not to some extent distorted. Its general shape and appearance suggests a *Notops*, or *Gastropus*, and in the absence of a fuller knowledge of its anatomy I have provisionally placed it in this genus under the above name. The figs. 1 and 2 of Plate LXXV. give an exact outline of its appearance in dorsal and lateral view, and I am indebted to my friend Mr. F. R. Dixon-Nuttall for these accurate drawings which he has made from the mounted specimen. Fig. 3 represents the jaws, which I have drawn under great difficulties and as accurately as was possible under the circumstances.

The anterior half of the body is stout, somewhat compressed dorso-ventrally, presenting a wide semicircular front with broad lateral lobes. The oral region appears to project prominently on the antero-ventral side; but it is quite possible that this appearance may be due to distortion, as the whole animal is not very well preserved. The posterior half of the body, which shows a deep



## VICTORIA NYANZA.

Only a very few collections from this lake were available; they were made near the shore at Bukoba on the west coast in April 1905, and from these I obtained the following 8 species of Rotifera, all of which are already known from this lake:—

- Monostyla bulla* Gosse.  
*Brachionus bakeri* Ehrenbg.  
 „ *fulcatus* Zach.  
 „ *forficula* Wierz.  
 „ *caudatus* Barr. & Dad.  
*Schizocerca diversicornis* var. *homoceros* Daday.  
*Anuraea aculeata* var. *valya* Ehrenbg.  
 „ *cochlearis* Gosse.

In this list the presence of a number of rare species of *Brachionus* is notable, a fact already noted by Prof. v. Daday. It is evident to me that a more thorough exploration of the micro-fauna of this vast and shallow lake would reveal a very considerable Rotatorian fauna.

Excluding the few species which could not be identified, the above lists contain 37 species of Rotifera collected by Dr. Cunningham in the great lake regions of Central Africa, of which 11 species were already known by the work of Dr. Collin and Prof. v. Daday, and 21 of these species were also previously recorded by me from South Africa, whilst one species is new to science.

## LAKE ALBERT.

Having also received for examination a very small tube of Plankton material collected with the tow-net in July 1907 in Lake Albert by Dr. R. T. Leiper, the Surgeon accompanying an expedition sent to this region by the Egyptian Survey Department, I will here record the three species of Rotifera found therein:—

- Monostyla bulla* Gosse.  
*Noteus quadricornis* Ehrenbg.  
*Brachionus bidentata* Anderson.

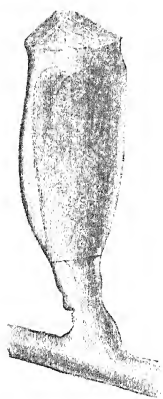
The last mentioned species appears to be very rare, having been found only once since its first discovery in Calcutta by Anderson in 1891, namely, in Bulgaria by Dr. Konsuloff (who sent me some specimens for identification) about two years ago.

DISTRIBUTION OF ROTIFERA IN CENTRAL AFRICA, being a list of all the species known from this region at the present time.

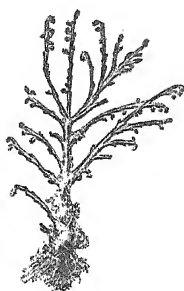
	Lake Tanganyika.	Lofu River.	Lake Nyasa.	Victoria Nyanza.	Lake Albert.	Drs. Collin & Daday's list of Victoria Nyanza Region.
<i>Ecistes mucicola</i> Kellicott .....	..	×				
<i>Rotifer vulgaris</i> Ehrenbg. ....	..	..	..	..	..	×
<i>Philodina emini</i> Collin .....	..	..	..	..	..	×
<i>Polyarthra platyptera</i> Ehrenbg. ....	×	..	..	..	..	×
<i>Triarthra longiseta</i> Ehrenbg. ....	..	×	..	..	..	×
<i>Synchaeta oblonga</i> Ehrenbg. ....	..	×	..	..	..	×
<i>Asplanchna intermedia</i> Hudson .....	×	..	..	..	..	×
<i>brightwelli</i> Gosse .....	..	..	..	..	..	×
<i>Notops macrourus</i> Barr. & Dad. ....	..	..	..	..	..	×
<i>lofuana</i> Rouss. ....	..	×	..	..	..	×
<i>Proales daphnicola</i> Thompson .....	..	×	..	..	..	×
<i>Copeus copeus</i> Ehrenbg. ....	..	..	..	..	..	×
<i>Tetramastix opoliensis</i> Zach. ....	..	..	..	..	..	×
<i>Rattulus longiseta</i> Schrank .....	..	×	..	..	..	×
<i>stylatus</i> Gosse .....	×	..	×	..	..	×
<i>gracilis</i> Tessin .....	..	×	..	..	..	×
<i>bicristatus</i> Gosse .....	..	×	..	..	..	×
<i>macerus</i> Gosse .....	..	×	..	..	..	×
<i>Diurella stylata</i> Eyfert .....	..	..	×	..	..	×
<i>Euchlanis hyalina</i> Hudson .....	..	×	..	..	..	×
<i>oropha</i> Gosse .....	..	×	..	..	..	×
<i>propatula</i> Gosse .....	..	×	..	..	..	×
<i>Monostyla lunaris</i> Ehrenbg. ....	..	×	..	..	..	×
<i>bullae</i> Gosse .....	×	..	..	×	×	×
<i>Cathypna leontina</i> Turner .....	..	×	..	..	..	×
<i>ungulata</i> Gosse .....	..	×	..	..	..	×
<i>luna</i> Ehrenbg. ....	×	×	..	..	..	×
<i>Salpina macracantha</i> Gosse .....	..	×	..	..	..	×
<i>brevispina</i> Ehrenbg. ....	×	..	..	..	..	×
<i>Pterodina trilobata</i> Shephard .....	..	×	..	..	..	×
<i>Noteus quadricornis</i> Ehrenbg. ....	..	×	..	..	×	×
" <i>var. brevispinus</i> Daday ..	..	×	..	..	..	×
<i>stuhlmanni</i> Collin .....	..	..	..	..	..	×
<i>Brachionus pala</i> Ehrenbg. ....	×	..	..	..	..	×
" <i>var. doreas</i> Gosse .....	..	..	×	..	..	×
<i>bakeri</i> Ehrenbg. ....	..	..	..	×	..	×
<i>falcatus</i> Zach. ....	..	..	..	×	..	×
<i>forficula</i> Wierz. ....	..	..	..	×	..	×
<i>caudatus</i> Barr. & Dad. ....	..	..	..	×	..	×
<i>angularis</i> Gosse .....	..	..	..	×	..	×
<i>rubens</i> Ehrenbg. ....	..	..	..	×	..	×
<i>militaris</i> Ehrenbg. ....	..	×	×	..	..	×
<i>bidentata</i> Anderson .....	..	..	..	×	..	×
<i>Schizocerca diversicornis</i> var. <i>homaceros</i> Daday ..	..	..	..	×	..	×
<i>Amurea aculeata</i> Ehrenbg. ....	×	..	..	..	..	×
" <i>var. valga</i> Ehrenbg. ....	..	×	×	×	..	×
<i>cochlearis</i> Gosse .....	..	..	×	..	..	×
<i>Notholca labis</i> Gosse .....	..	..	×	..	..	×
<i>Pedalion mirum</i> Hudson .....	..	..	..	..	..	×







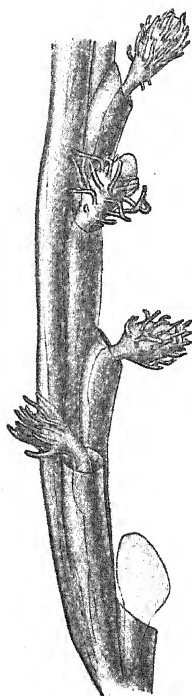
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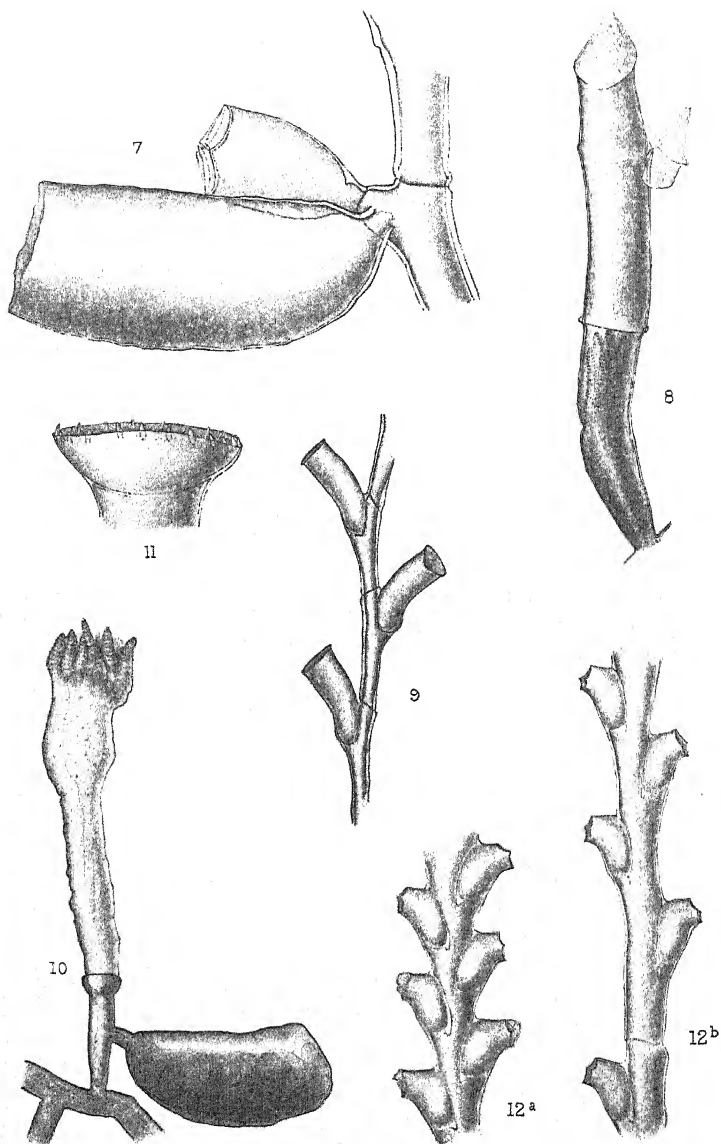
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HYDROIDS FROM MERGUI ARCHIPELAGO





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3. ROUSSELET, C. F.—“Contribution to our Knowledge of the Rotifera of South Africa.” Journ. Royal Micr. Soc. 1906, pp. 393-414.

## EXPLANATION OF PLATE LXXV.

- Fig. 1. *Notops Iofuana* Rousselet, dorsal view.  $\times 360$ .  
 2.    ”       ”       ”       lateral view.  $\times 360$ .  
 3.    ”       ”       ”       the jaws.  $\times$  about 700.

3. The Marine Fauna of the Mergui Archipelago, Lower Burma, collected by Jas. J. Simpson, M.A., B.Sc., and R. N. Rudmose-Brown, D.Sc., University of Aberdeen, February to May 1907.—The HYDROIDS. By JAMES RITCHIE, M.A., B.Sc., Natural History Department, The Royal Scottish Museum \*.

[Received April 28, 1910.]

(Plates LXXVI. & LXXVII.†, and Text-fig. 79.)

The Hydroids were represented in the collections brought together in the Mergui Archipelago by Dr. John Anderson in 1882, and described in the Journal of the Linnean Society for 1889, by a meagre total of six species, two of which were regarded by Hincks as new. The reasonable anticipation that the careful collecting of Dr. Brown and Mr. Simpson would add many species to the Hydroid fauna of this region of the Indian Ocean has been amply fulfilled; for the present collection, confined to a littoral area, contains representatives of thirty species, only three of which (*Campanularia raridentata* and *Idia pristis*, both widely distributed species, and *Aglaophenia crispata*, a synonym of *Lytocarpus pennarius*, *vide* Billard, 1909, p. 329) were included in Hincks's list.

As only two of the species, being described as new to science, must be regarded as peculiar to the Archipelago, the collection is well fitted to show the relationship which the Hydroid fauna bears to that of neighbouring seas. Leaving out of account an undetermined species of *Plumularia*, nineteen of the Mergui species have already been recorded from the Indian Ocean, the majority of these occurring off Madagascar and the eastern shores of Africa. The remaining ten species, indicated by

\* Communicated by R. KIRKPATRICK, F.Z.S.

† For explanation of the Plates see p. 825.

asterisks in the following list, have thus been added to the fauna of the Indian Ocean. As to the wider relationships:— Three species are peculiar to the Indian Ocean (*Corydendrium sessile*, *Hebella crateroides*, *Calycella oligista*), leaving twenty-six to be accounted for. Of these, twelve are so widely distributed that their occurrence, emphasizing the normal nature of the fauna, can give no indication of special affinity: three being found in the Atlantic and North Pacific Oceans and in Australasian seas (*Opercularella lacerta*, *Plumularia setacea*, *Antenella secundaria*); two in the Atlantic and North Pacific Oceans (*Perigonimus repens*, *Campanularia raridentata*); and seven in the Atlantic Ocean and in Malay-Australian seas (*Pennaria disticha*, *Halecium tenellum*, *Campanularia corrugata*, *Hebella calcareata*, *Sertularella polyzonias*, *Idia pristis*, *Diphasia digitalis*). Of the remaining fourteen, four have been found only in the Atlantic Ocean (*Eudendrium attenuatum*, *Cuspidella costata*, *Lafœa serrata*, *Lafœa venusta*), seven in the Malay-Australian area (*Eudendrium generalis*, *Cladocoryne haddoni*, *Halecium simplex*, *Thyroscyphus vitiensis*, *Sertularella cylindrica*, *Sertularella quadridens*, *Sertularia turbinata*), one in the North Pacific Ocean (*Thyroscyphus regularis*), and two in both the last-named areas (*Lytocarpus pennarius* and *L. phoeniceus*).

The closer relationship is obviously with the fauna of the Pacific Ocean (represented by ten distinctive species), and in particular with the Malay-Australian portion of that ocean (represented by seven species). The significance of the apparent Atlantic affinity is minimised when it is understood that of the four species common to it and the Mergui Archipelago, one (*Eudendrium attenuatum*) is identified with much doubt, while the remaining three are very minute epizoid species, the presence of which in other regions may conceivably have been overlooked.

It is remarkable that of the thirty species recorded, seventeen were found climbing upon larger Hydroids and one upon a Polyzoon, the majority being minute, habitual epizoa, belonging in the main to the families Halecidae, Campanularidae, Campanulinidae, and Lafœidae. The examination of this collection, and of others, leaves with me the distinct impression that the epizoid Hydroids are not distributed indiscriminately upon all types of Hydroid host. Thus, in general, the members of the family Plumularidae remain comparatively free from extraneous growths—a fact to be correlated, perhaps, with their possession of nematophores; while colonies, belonging especially to the family Sertularidae, are occasionally so overgrown that the structures of the host are much obscured. Even distinct preferences for certain species may be observed. Taking, for each epizoid species in this collection, the total numbers of stations at which it was found, and adding those numbers for all the epizoid species, we find that epizoid species were found at a sum total of forty-five stations. At thirty-two of these *Idia pristis* was either the only host, or one of the hosts where more than one species

was infested; *Thyroscyphus vitiensis* at nine; *Sertularella quadridens* at four; *Corydendrium sessile*, *Eudendrium attenuatum*, *Lytocarpus phoeniceus* each at two; and *Diphasia digitalis* and *Plumularia setacea* each at one. This result bears out the impression gained from handling the collection, that *Idia pristis* is remarkably subject to infestation by extraneous Hydroid colonies. Frequently its hydrothecæ were all but obscured by the attendant growths of Hydroids and Polyzoa, and this although the state of the hydranths and of the cœnosarc generally, indicated that the host colony was in a perfectly healthy condition.

The occurrence, in *Lafoëa venusta* (?), of what appears to be a step towards a more intimate symbiosis; of a canaliculated cœnosarc in the stem and branches of *Sertularella quadridens*; of the hitherto undescribed gonosomes of *Halecium simplex* and *Thyroscyphus regularis*, are worthy of notice.

Finally, I would express my thanks to Dr. R. N. Rudmose-Brown and Mr. J. J. Simpson for entrusting this collection to me for examination.

### *List of Species.*

#### I. Gymnoblastea.

##### Family CLAVIDÆ.

\**Corydendrium sessile*, sp. n., p. 802.

##### Family BOUGAINVILLIDÆ.

\**Perigonimus repens* Wright, p. 804.

##### Family EUDENDRIDÆ.

\**Eudendrium attenuatum* Allman (?), p. 804.

" " *generalis* Lendenfeld, p. 805.

##### Family CORYNIDÆ.

*Cladocoryne hadlioni* Kirkpatrick, p. 805.

##### Family PENNARIDÆ.

*Pennaria disticha* Goldfuss, var. *australis* Bale, p. 806.

#### II. Calyptoblastea.

##### Family HALECIDÆ.

\**Halecium simplex* Pictet, p. 807.

" *tenellum* Hincks (?), p. 808.

##### Family CAMPANULARIDÆ.

*Campanularia corrugata* Thornely, p. 809.

" *varidentata* Alder, p. 809.

*Hebella calcarata* A. Agassiz, p. 810.

" *crateroides* Ritchie, p. 810.

*Thyroscyphus regularis* Jäderholm, p. 811.

" *vitiensis* Marktanner, p. 812.

## Family CAMPANULINIDÆ.

\* *Opercularella lacerta* Johnston, p. 812.\* *Calycella oligista*, sp. n., p. 813.*Cuspidella costata*, Hincks, p. 814.

## Family LAFOËIDÆ.

*Lafoëa serrata* Clarke, p. 815.\* „ *venusta* Allman (?), p. 815.

## Family SERTULARIDÆ.

\* *Sertularella cylindrica* Bale, var. *pusilla*, n., p. 817.\* „ *polyzonias* L., var. *cornuta* Ritchie(?), p. 818.\* „ *quadridens* Bale, p. 818.*Idia pristis* Lamouroux, p. 820.*Diphasia digitalis* Busk, p. 821.*Sertularia turbinata* Lamouroux, p. 821.

## Family PLUMULARIDÆ.

*Plumularia setacea* Linn. (?), p. 822.

„ sp. indet., p. 822.

*Antenella secundaria* Gmelin, p. 822.*Lytocarpus pennarius* Linn., p. 822.„ *phœniceus* Busk, p. 823.

\* indicates a species recorded for the first time from the Indian Ocean.

## SYSTEMATIC DISCUSSION.

## I. GYMNOBLASTEA.

## Family CLAVIDÆ.

CORYDENDRIUM SESSILE, sp. n. (Plate LXXVI. figs. 1 &amp; 2.)

TROPHOSOME.—Colony small, the largest of the three collected being only 37 mm. in height. The stem is strongly fasciated, 1.5 mm. thick towards the base, and straight. It may divide into main branches, which are beset by numerous smaller, almost equal branchlets, about 1 mm. in length. These spring from two opposite sides, and lie roughly in one plane. The branchlets on any one side are almost equidistant from each other, but their positions bear no regular relation to those of the opposing series. They taper very slightly towards the base, but there is no trace of ringing nor of wrinkling.

The majority of the hydranths spring from tubes on the anterior surface of the branchlets, although a few are also scattered on the main branches. The hydranth tubes do not become free from the common fascicle, except rarely and for an extremely short distance; nor are special hydrophore-like portions developed. Thus the hydranth projects simply from the open mouth of a tube, the adcauline wall of which is adnate. The hydranth tubes

are arranged in two series, the polyps of one series alternating with those of the other. The aperture faces outwards and upwards, is slightly elliptical in shape, and has an even margin, indicating the boundary between the thicker perisarc and the place where the chitinous coat becomes so thin and delicate that it follows the movements of the polyp. The perisarc throughout is covered by a thin coating of extraneous material—diatoms, sand-grains, fragments of sponge-spicules, and such like.

The hydranths are much contracted, and in this state exhibit a pyriform body with well-developed hypostome. The tentacles appear to number about forty.

GONOSOME unobserved.

Colour, in alcohol, grey.

Dimensions:—

Diameter of branchlets immediately above origin	0.31–0.38 mm.
„ hydranth tube .....	0.25–0.31 mm.
Hydranth, length .....	0.52–0.98 mm.
„ diameter .....	0.21–0.42 mm.
Nematocysts on tentacles, length .....	5 $\mu$ .
„ „ breadth .....	3 $\mu$ .

*Locality.* Three small colonies, with hydrorhiza embedded in a sponge, were found at St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand.

So little is known of the variation liable to occur in the individual species of this genus, that it is difficult to fix on definite specific characters. In this case, I have relied mainly on the structure of the tubes from which the hydranths project. In the majority of the species of *Corydendrium* so far described these are free for a considerable distance below the hydranth: but here the tubes are adnate up to the end. This gives to the branches a dumpy appearance, unlike the lax growth of other species. In this respect it approaches most closely *C. corrugatum* Nutting (1905, p. 941), which is to be distinguished, however, by its distinct “hydrophore-like structures,” which are “usually distinctly corrugated with deep irregular annulations”; by the presence of a well marked annular constriction near the origin of the branches; and by the large size (5 inches) of the colonies.

The species, *Soleniopsis dendriformis*, described by me in 1907 (1907, p. 494) as representing a new genus, under the erroneous supposition that *Corydendrium* gave rise to gonophores with free medusæ—I had been unable to refer to the magnificent description of Weismann (1883),—obviously belongs to the genus *Corydendrium*, as Dr. Stechow has recently pointed out (1909, p. 9).

*Corydendrium dendriformis* differs from *C. parasiticum* in possessing thick, definite stems, with branchlets arranged in pseudo-pinnate fashion, and in having the free portion of the tubes from which the hydranths project much shorter than those of *C. parasiticum*.



## Family BOUGAINVILLEÆ.

## PERIGONIMUS REPEXS Wright, 1858.

Rare examples of an epizoic species occur, which cannot be specifically distinguished from British specimens of *P. repens*, the simple lax habit of which they exactly assume. There are differences between the dimensions of the Mergui and of British examples; for while the former are smaller in height and in the proportions of their hydranths and hydrocaulus, in respect of the nematocysts in the tentacles the order is reversed. The comparative table which follows shows at a glance the size-relations of the two forms. About twelve tentacles crown each hydranth.

No trace of gonosome was observed.

Dimensions:—

	Mergui specimen.	Typical Scottish example*.
Height of colony .....	3 mm.	6 mm.
Diameter of hydrocaulus .....	0.04 mm.	0.07 mm.
Hydranth, length .....	0.17–0.24 mm.	0.24–0.34 mm.
„ greatest breadth .....	0.08–0.13 mm.	0.14–0.15 mm.
Nematocysts of tentacles, length	5.5 $\mu$ .	4.5 $\mu$ .
„ „ breadth	3 $\mu$ .	2.2 $\mu$ .

*Locality.* Rare colonies epizoic on *Corydendrium sessile*, from St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand.

The present record adds *P. repens* to the fauna of the Indian Ocean. It has already been noted from the eastern and western sides of the North, and the western side of the South Atlantic Ocean, from the Mediterranean Sea, and from the eastern and western (Japan: Stechow, 1909, p. 25) sides of the Pacific Ocean.

## Family EUDENDRIÆ.

## EUDENDRIUM ATTENUATUM Allman (?), 1877.

Many poor colonies, lacking any trace of hydranth or gonosome, I refer, with uncertainty, to this species, on account of resemblance in the skeleton. The Mergui specimens attain a somewhat greater length (3 inches) than the original examples; but the delicate, very slender, non-fascicled stems, with their few branches, and their short hydranth-bearing ramules lying in one plane and set alternately at regular intervals of about 1 mm., are very similar in both cases. Three or four rather irregular annulations mark the base of each ramule, and occasionally a few odd rings occur irregularly on the ramules and on the stem itself. The regular and close alternation of the hydranth-bearing ramules seems the most evident character of an indefinite species, though a somewhat similar arrangement is observed in *E. maldivense* Borradaile (1905, p. 838).

\* Slide of specimen from Loch Carron, 60 fathoms, in my collection.

Dimensions :—

Stem, diameter ..... 0.20-0.24 mm.

Hydranth-bearing ramules, diameter . 0.11-0.16 mm.

*Localities.* Many colonies from St. 22, Hastings Harbour, 3 to 20 fathoms and shore, rock and sand; and a few poor colonies, paler in colour, from each of Stations 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; and 25, Gregory Group and Crichton Island, 4 to 14 fathoms, stones and broken shells, and rock.

Recorded originally by Allman from S.S.W. of Tortugas, at a depth of 60 fathoms, this doubtful species forms an addition to the fauna of Indian seas.

#### EUENDRIUM GENERALIS Lendenfeld, 1885.

The colonies belonging to this species are mature, but are only about 1 cm. in height. They bear well-developed female gonophores, oval in shape, which spring in a whorl of four or five from the base of a hydranth, as in Kirkpatrick's description and figures (1890, p. 607, pl. xv. fig. 2).

The trophosome of this species is hard to distinguish from that of *E. capillare*. The more slender character of the branches of the latter, relied on in part by Kirkpatrick, is of little value, since a considerable amount of variation occurs in both species. On the other hand, the branching of *E. capillare* is more profuse, and irregular; also in the Australian species there is, in the smaller branches, distinct alternation, while the whole colony appears more rigid than the lax growths of *E. capillare*.

Dimensions :—

Stem, diameter ..... 0.14 mm.

Hydranth-bearing ramule, diameter ..... 0.09 mm.

*Locality.* Creeping in small quantity upon *Euendrium attenuatum*? and *Idia pristis*, both from St. 22, Hastings Harbour, 3 to 20 fathoms and shore, rock and sand.

Until the present record from the Indian Ocean, this species has been found only in the Australian region: Port Phillip, near low water (Lendenfeld, 1885, p. 351); Torres Straits—20 miles N.N.W. of Warrior Island, 5½ fathoms; Murray Island, 15 to 20 fathoms (Kirkpatrick, 1890, p. 607).

#### Family CORYNIDÆ.

##### CLADOCORYNE HADDONI Kirkpatrick, 1890.

Except in size (for they are even more diminutive than those recorded by Kirkpatrick and Jüderholm), the Mergui specimens agree with the description and figures of the former, the double wrinkle at the base of the stalk being very evident. On occasion, one or two additional wrinkles may occur at the base of the stalks and, more seldom, on their middle portions; but in the majority of cases these rings are of little significance, since they belong to a new stalk regenerated after the destruction of the old one. Here,

as in simple Campanularian hydroids, regeneration is not content with simply adding a portion to the old stalk, but a complete new stalk is reproduced, springing from within the truncated end of the old one.

Dimensions:—

Stalk, length .....	0.43–0.98 mm.
„ diameter .....	0.06–0.08 mm.
Stolon, diameter .....	0.10 mm.
Hydranth, length.....	0.34–0.36 mm.
„ greatest breadth .....	0.11–0.21 mm.

Cnidoblast threads, armed with barbs such as Kirkpatrick has figured, accompany several of the hydranths. They are remarkable for their large size, the barbed portion being  $6\mu$  in diameter from tip to tip of the barbs.

*Localities.* Rare hydranths on *Thyroscyphus vitiensis* and on *Idia pristis* from St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud. A solitary hydranth on *Idia pristis* and a few on *Corydendrium sessile* from St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand.

The species has been previously recorded only from Murray Island, Torres Straits, 15 to 20 fathoms (Kirkpatrick, 1890, p. 606); and, in Indian seas, from Paumben, 1 to 3 fathoms (Jäderholm, 1903, p. 263).

#### Family PENNARIDÆ.

\*PENNARIA DISTICHA Goldfuss, 1820. Var. AUSTRALIS Bale, 1884.

(= *Pennaria carolinii* Ehrenberg, 1832.)

A few well preserved colonies, the largest 30 mm. high, represent this species. The ramules from which the hydranths project increase considerably in diameter upwards from their origin, where they bear three or four annulations, to the distal end, which is smooth. The number of filiform tentacles varies from nine to twelve, but there is much variation in the number of the capitate tentacles. The numbers depend, to some extent, upon the age of the hydranth, for the tentacles are fewest in those hydranths which, springing from ramules, lie towards the distal end of a branch—that is, in the youngest hydranths; for growth proceeds by the elongation of a branch, new polyps coming into being next to the terminal polyp, which is the oldest and the largest on the branch.

Pictet's careful comparative study of colonies of typical *P. carolinii* from Naples, and of typical *P. australis* from Amboyna, makes clear that the latter form falls within the range of variation observed in the former species. But so definitely limited is the basal ringing of the ramules from which the hydranths arise, and so great a difference is there

\* For synonymy, see Bedot, 1901, p. 459.

in the proportions of the European and the Indo-Pacific forms, that I retain for the latter a distinct varietal name.

*Locality.* St. 29, reef off High Peaked Island, shore.

Although *P. cavolinii* in its varying forms has been recorded from Eastern Australia (Bale, 1884, 1893; Lendenfeld, 1885), and from the East Indies (Pictet, 1893; Campenhausen, 1896; Weltner, 1900), the only records for the Indian Ocean are those of Warren (1906, 1907, and 1908, as *Halocordyle cooperi*, syn. *Pennaria australis*, var. *cooperi*) and that from Christmas Island in the paper following.

## II. CALYPTOBLASTEA.

### Family HALECIDÆ.

*HALECIUM SIMPLEX* Pictet, 1893. (Plate LXXVII. figs. 10 & 11.)

This very rare species is represented by closely woven colonies covering the surface of a Polyzoon which is clustered at the base of colonies of *Corydendrium sessile*. The presence of the gonosome, so far undescribed, renders these specimens of particular interest.

**TROPHOSOME.**—To the naked eye the minute colonies are almost invisible, the hydranths being most easily discerned as they project from the surface on which the colonies grow, in close groups, resembling clusters of the smaller species of the entoproctan polyzoon, *Pedicellina*.

The stolon strands are of small diameter, but can often be traced for a considerable distance. Their courses are complicated, however, by the occurrence of offshoots, which, uniting with other stolons, form a network which lies closely upon the substratum, or is interwoven with it.

Short, unbranched, unwrinkled hydrocauli arise from the stolon at short distances from each other. Basally their diameter is small, but it gradually increases until, at the base of the hydrotheca, the girth of the hydrocaulus is about equal to that of the stolon. The hydrothecæ are very small. Their walls, which are well developed, form an inward curve to the margin, so that, instead of being flaring or trumpet-shaped, as in many species of *Halecium*, they are rather saucer-shaped. Very close to the margin occurs a ring of bright dots, chitinous prominences on the inner surface of the hydrotheca to which the hydranth was attached. Here the internal prominences are more highly developed than in any other species I have examined, for they sometimes rise into pronounced spines 7  $\mu$  in length (Pl. LXXVII. fig. 11). Occasionally two or even three hydrothecæ occur in succession, a new hydrocaulus arising from within an old hydrotheca.

The hydranth is of great size. When contracted it is about twice as long as the hydrocaulus, but when extended it reaches a length of one millimetre or even more. It consists of a long

cylindrical neck, the base of which is attached to the hydrotheca at the chitinous projections already described. Distally this swells out into a very definite bulb, which is surmounted by a circle of from 18 to 20 tentacles. At the bases of the tentacles a ring of very large bean-shaped nematocysts,  $30\ \mu$  long by  $6\ \mu$  broad, surrounds the hydranth. Similar cells occur in the cenosarc of hydrocaulus and stolon.

**GONOSOME.**—This does not appear to have been described. A gonangium arises from the side of the hydrocaulus, about half-way between the hydrotheca and the stolon. The female gonangium is borne on a short stalk, and is roughly calceolate in shape, resembling the female gonangium of *H. beanii*, except that here the tubular orifice of the upper surface does not occur. All the gonangia I have examined contain ova to the number of about six. The male gonangium, therefore, remains unknown.

Dimensions:—

Stolon, diameter .....	0.06–0.07 mm.
Hydrocaulus, length .....	0.18–0.28 mm.
Hydrotheca, depth .....	0.024–0.027 mm.
„ diameter at margin .....	0.08–0.10 mm.
Gonangium, length .....	0.42–0.50 mm.
„ greatest diameter .....	0.17–0.21 mm.
Hydranth, length extended .....	1.05 mm.
„ „ contracted .....	0.78 mm.

**Locality.** Epizoid on a polyzoon associated with *Corydendrium sessile*, from St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand.

Hitherto recorded only from Amboyna, in the Moluccas (Pictet, 1893, p. 22), this record adds the species to the fauna of Indian seas.

#### HALECIUM TENELLUM Hincks (?), 1861.

The trophosomes are lax in habit, and in all other respects agree with Hincks's species; but, in the absence of the gonosome, confident identification is impossible, especially since the likeness between the trophosomes of young examples of the Australian *H. parvulum* Bale and *H. tenellum* appears to be almost perfect (see Markt.-Turner., 1890, p. 218).

Dimensions:—

Stem, diameter .....	0.045 mm.
Hydrotheca, depth .....	0.024–0.030 mm.
„ diameter at margin .....	0.099–0.108 mm.

The dimensions of the Mergui specimens are considerably smaller than those of British examples.

**Localities.** Epizoid on *Thyroscyphus vitiensis* from Stations 15 and 16, Ravenshaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud.

Recorded with some doubt from Eastern Australia by Bale (1884, p. 65) and Lendenfeld (1885, p. 405), this widely dis-

tributed species has been described from the Indian Ocean only by Billard, from Macalunga, Mozambique, 22 metres (1907 *b*, p. 338).

### Family CAMPANULARIDÆ.

#### CAMPANULARIA CORRUGATA Thornely.

Except at Station 1, where it was also associated with *Sertularella quadridens* and *Diphasia digitalis*, this species always occurred as an epizoon on *Idia pristis*.

*Localities.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; short and stout, strongly ribbed hydrothecæ on *Diphasia digitalis*, and long, cylindrical individuals on *Idia pristis*. Stt. 15 and 16, Ravenshaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud; occasionally. St. 22, Hastings Harbour, shore to 20 fathoms, rock and sand; fairly common. St. 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; not common. St. 25, Gregory Group and Crichton Island, 4 to 14 fathoms, stones and broken shells and rock; rare cylindrical hydrothecæ with short stalks. St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand; rare.

#### CAMPANULARIA RARIDENTATA Alder, 1857.

From British examples the majority of the specimens here referred to *C. raridentata* differ in lacking the swelling which intervenes between the base of the stalk and the stolon, in this respect resembling examples recorded from areas so wide apart as Calbuco, South America (Hartlaub, 1905, p. 567), St. Malo, France (Markt.-Turner., 1890, p. 205), and the Indian Ocean (Hincks, 1889, p. 133, *cf.* pl. xii. fig. 5). From seven to eleven rings occur at the base of the stem, and from three to five underneath the hydrotheca, and sometimes a few annulations mark also the middle portion of the stem. The margin of the hydrotheca appears to be divided into from five to seven large teeth, the extreme tenuity and transparency of which render them difficult to observe. The hydranth bears twelve to thirteen tentacles.

No gonosome was observed.

The dimensions of the Mergui specimens are much less than those of St. Malo specimens recorded by Marktanner-Turner-etscher (1890, p. 205), and approach most closely those of a single example from Saint-Vaast described by Billard (1907 *a*, p. 173), with which they also agree in possessing few hydrothecal teeth.

Dimensions, in mm.:—

	St. 1.	St. 23.
Stem, length .....	0.59	0.35-0.45
„ diameter .....	0.07	0.04-0.06
Hydrotheca, depth .....	0.50	0.29-0.41
„ diameter at mouth .....	0.17	0.13-0.15

*Localities.* St. 1, east of Tavoy Island and Port Owen, 4-12 fathoms, sand and broken shells, and mud; rare. St. 25, Five Islands, 8 to 12 fathoms, rock and sand, and mud; rare. St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand; rare.

Except from St. 23, where this species also occurs on *Sertularella quadridens*, specimens are confined to *Idia pristis*.

From each of Stations 1 and 28 comes a solitary simply-stalked hydrotheca with cone-shaped basal portion, surmounted by almost cylindrical walls terminating in seven or eight sharp teeth. The structure of the basal portion resembles that of the hydrotheca of *Obelia andersoni* Hincks, but I regard the present specimens as abnormally developed examples of *C. raridentata*.

#### HEBELLA CALCARATA A. Agassiz, 1865.

One of the most widely distributed of the species in the collection, occurring at eight of the fourteen stations from which Hydroids were obtained. It shows considerable diversity of form, being usually represented by the long smooth hydrothecæ of the typical form, but frequently assuming the shape of the variety recorded by Marktanner (1890) as *Lafoëa contorta*. This epizoic species, like several others, shows a remarkable constancy of preference for *Idia pristis*, seeing that at all stations, with the exception of Station 9, where it was creeping on *Thyroscyphus vitiensis*, it occurred on that species, and on it alone.

*Localities.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; not common, often var. *contorta*. St. 9, between Bentinck Island and Courts Island, 12 to 26 fathoms, sand and shells. St. 14, Bushby Island pearling-ground, shore to 21 fathoms, sand and mud; rare. Stt. 15 and 16, Ravenshaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud; occasionally present, often assuming the shape of var. *contorta*. St. 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; very common, mostly var. *contorta*. St. 25, Gregory Group and Crichton Island, 4 to 14 fathoms, stones and broken shells, and rock; very rare. Moskos Islands, 3 to 26 fathoms, rock and sand, or rock and mud; common.

#### HEBELLA CRATEROIDES Ritchie, 1909 b.

The hydrothecæ are smaller than those of the type specimens from the Andaman Islands. The hydranths are decayed, and no gonosome was observed.

Dimensions:—

Hydrotheca, depth .....	0.20 mm.
„ diameter at mouth.....	0.15-0.17 mm.

*Localities.* Stt. 15 and 16, Ravenshaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud; rare, on *Lytocarpus phæniceus*.

THYROSCYPHUS REGULARIS Jäderholm, 1896. (Plate LXXVII. fig. 7.)

(*T. equalis* Warren, 1908.)

TROPHOSOME. The specimens are somewhat larger than those originally described, sometimes almost 20 cm. in length, while the branches may reach a length of 45 mm., in place of the maximum of 18 mm. given by Jäderholm.

The species is readily distinguished from *T. vitiensis* by the presence of a very distinct operculum, accompanied by deep bays round the margin; further, the bright rim runs in this case much nearer to the edge, and is not so pronounced, while the faint ringing at the internodes is more marked. The joints, varying in number, which are said to occur on the peduncle, are only occasionally present (though sometimes up to three or four were observed), and even then they are not essential to the specific structure, for they are due to the destruction of the hydrotheca, and to the subsequent regeneration of a new hydrotheca from within the remains of the old one, the apparent joints being the reliquæ of former calycles. No specific value can attach to these accidental "joints," the like of which I have already observed in *Thyrosocyphus simplex* = *tridentatus* (1909, p. 75, fig. 1 b) and in *Lytoscyphus marginatus*; but in *T. ramosus* the semblance of a twist occurs in the peduncle.

The minute structure of the cœnosarc is obscured by the presence of opaque granules which occur in great abundance. In these specimens the hydranth is attached, not to a continuous ridge, as in the specimens from Natal, which Warren has described as *T. equalis* (and which I am unable to distinguish from *T. regularis*), but to a row of small chitinous prominences which runs round the inside of the hydrotheca in an exceedingly sinuous curve, having two maxima, one on the adcauline, the other on the abcauline surface, and two lateral minima.

GONOSOME. Gonangia, which have not previously been described, were found on a single colony from Station 25 (Pl. LXXVII. fig. 7). The cœnosarc has disappeared, but the perisarc is in the form of a long cylinder, larger even than that of *T. torresii* (see Jäderholm, 1903, p. 273). Very indefinite and irregular wrinkles appear on the perisarc. The insignificant stalk of the gonangium arises from the projection of the internode upon which a hydrotheca is perched

Dimensions:—

Branch, diameter .....	0.36 mm.
Distance between hydrothecæ .....	1.13 to 1.3 mm.
Hydrotheca, depth .....	0.96 mm.
"      breadth at mouth .....	0.63 mm.
Peduncle, diameter.....	0.20 mm.
Gonangium, length.....	3 mm.
"      breadth .....	1 mm.

*Localities.* A large bunch of colonies from St. 22, Hastings



Harbour, shore to 20 fathoms, rock and sand. St. 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; two colonies. St. 25, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand; many colonies.

This species has already been recorded from the China Sea (Jäderholm, 1896, p. 9), and from Bird Island, Algoa Bay, Cape Colony (Warren, 1908, p. 344, as *T. aequalis*).

*THYROCYPHUS VITIENSIS* Marktanner-Turneretscher, 1890.

A widely distributed species, occurring at eight of the fourteen stations from which Hydroids were obtained. In this, as in *T. regularis*, the hydranth is attached to a row of minute chitinous prominences on the inside of the lower portion of the hydrotheca. These are arranged as in the previous species, but they are more strongly developed, and are placed on a slightly raised portion of the hydrothecal wall.

*Localities.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; common. St. 3, French Bay, King Island, and south end of Iron Island, 3 to 8 fathoms, mud and rock, or sand; common. St. 9, between Bentinck Island and Courts Island, 12 to 26 fathoms, sand and shells; rare. St. 14, Bushby Island pearling-ground, shore to 21 fathoms, sand and mud; rare. Stt. 15 and 16, Ravenshaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud; rare. St. 19, Paye Island and Pink Island, 7 to 9 fathoms, rock and sand; rare. St. 25, Gregory Group and Crichton Island, 4 to 14 fathoms, stones and broken shells, and rock; fairly common. St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand; rare.

Family CAMPANULINIDÆ.

*OPERCULARELLA LACERTA* Johnston, 1847.

Identification depends upon trophosome characters alone, the gonosome being absent. I can detect nothing, however, which could distinguish these specimens from North Sea examples of the above species. It occurs in its simplest form, a creeping stolon, sending up here and there short ringed stalks, on each of which is poised an exceedingly hyaline hydrotheca.

Dimensions:—

Hydrotheca, depth *	0.21 mm.
diameter	0.08–0.09 mm.
Peduncle, diameter	0.04 mm.

*Locality.* Moskos Islands, 3 to 26 fathoms, rock and sand, or rock and mud; rare, growing on a stem of *Plumularia setacea*.

Although the range of the species is a wide one, for it has been recorded from the North of Europe, from both sides of the

\* From top of operculum.

North Atlantic Ocean, and from the Western Pacific (China and Eastern Australia), it has not hitherto been found in the Indian Ocean.

CALYCELLA OLIGISTA \*, sp. n. (Plate LXXVI. figs. 3 & 4.)

**TROPHOSOME.** The colony is epizoaic, and consists of a creeping, delicate stolon which lies in close contact with the specimen upon which it occurs. From this stolon hydrothecæ spring at irregular intervals.

The hydrothecæ are exceedingly minute, delicate, hyaline, and transparent, without a trace of the smoky tint which characterises *C. syringa*. In shape they are tubular and cylindrical, of approximately the same diameter for the greater portion of their length, although the proximal half is usually slightly bulged, and tapers, more or less rapidly, to join the stalk. The margin of the hydrotheca, which is very slightly everted, is definite, and is of considerable strength, for it is seldom that it is found in a collapsed condition. It is divided into shallow crenulations, similar to those in *C. syringa*, each of which subtends the base of an opercular valve. In no case was a duplication of the margin noticed. The operculum is distinct from the hydrothecal wall, and is composed of about twelve to fourteen exceedingly delicate valves, difficult to distinguish. The cavity of the hydrotheca is separated from that of the stalk by a distinct but delicate diaphragm. The stalk is usually very short, so that the hydrotheca almost rests on the stolon, but in one case (Pl. LXXVI. fig. 3) a well developed stalk was observed. This stalk was marked by a few irregular indentations, but in other cases the stalks were smooth, and ringing of a regular nature never occurred.

The hydranth is large compared with the size of the hydrotheca. It is attached by a basal disk to the hydrothecal wall immediately above the diaphragm, and is continued upwards as a cylindrical body with conical hypostome, surrounded by a whorl of about seven to ten tentacles. The ectoderm is thick, and the tentacles, in contraction, are dumpy and stout.

The gonosome was not observed.

Dimensions:—

Stolon, diameter .....	30 $\mu$ .
Hydrotheca, depth .....	120–138 $\mu$ .
„ greatest diameter .....	45–66 $\mu$ .

**Localities.** St. 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; very rare, on *Idia pristis*. St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand; very rare, on *Idia pristis* and *Thyroscyphus vitiensis*.

**Systematic position.**—This species differs remarkably in size, colour, texture, and in the development of the peduncle and its ringing from *C. syringa*, although there is a similarity between

\* *ὀλίγιστος*, smallest.

its hydrothecæ and some of the varieties of the latter species (see Broch, 1909 *b*, text-fig. 22). It approaches most closely *C. nuttingi* Hargitt (1909, p. 378), from which it differs in being smaller in size, in being cylindrical instead of tapering from hydrothecal margin to base, and in lacking distinctly annulated peduncles, with "annulations occasionally extending some distance (rarely over the entire body) on the thecal walls."

I regard the unnamed specimen, mentioned and figured by Miss Thornely (1908, p. 83, pl. ix. fig. 5), from Khor Shinab, 10 to 12 fathoms, in the Soudanese Red Sea, as belonging to this species.

CUSPIDELLA COSTATA Hincks, 1868. (Plate LXXVII. fig. 8.)

To the short and incomplete description given by Hincks the following observations may be added. The hydrotheca is cylindrical for the greater part of its length, but near the base it gradually tapers downwards. Frequently the basal portion of the hydrotheca lies along the object upon which the epizoon is growing, the distal portion bending upwards at an angle, slightly after the manner of *Lafôea serrata*. Within the bent portion the retracted polyp is generally found. Similar bent hydrothecæ have been described by Dr. Billard from La Hougue (1904, p. 165).

The lines of growth held to be characteristic of the species, and clearly marked in our specimens, are not lines of growth in the ordinary sense, marking the place where new growth has commenced. They indicate, instead, the margins of earlier hydrothecæ, the opercular flaps of which occasionally remain attached and give an appearance of longitudinal fluting to the succeeding portion of the hydrotheca, as is suggested in the terminal segment in Hincks's figures (1868, pl. xl. figs. 5, 5*a*). The secondary hydrotheca (produced probably on the regeneration of an entirely new hydranth) lies within the primary, and for some distance their walls, though in close contact, remain distinct. The tertiary, when such occurs, lies within the secondary, and so on. Thus the terminal segment is, as Hincks observes, "of thinner material than the rest," for its walls are those of a single hydrotheca, while proximal to the uppermost segment the walls, owing to the telescoping arrangement, are considerably strengthened. It is noteworthy that the proximal segment is usually of distinctly less calibre than its successors. The operculum of the hydrotheca is composed of about 14 or 15 flaps.

The hydranth is strongly retractile, retiring on contraction to the proximal third of the hydrotheca. It appears to have about six to eight tentacles, which are closely set with whorls of large oval nematocysts, the whorls being  $7.5\mu$  apart. The average size of the nematocysts in these whorls is  $5.2\mu$  long by  $2\mu$  broad, but at the tip of the tentacle larger examples occur,  $10.5\mu$  long by  $5\mu$  broad.

No gonosome was observed.

Dimensions:—

Hydrotheca, length .....	0·7–1·12 mm.
„ diameter .....	0·10–0·14 mm.
Length of flaps of operculum .....	0·11–0·13 mm.

*Localities.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; rare hydrothecæ on *Thyroscyphus vitiensis*. St. 3, French Bay, King Island, and south end of Iron Island, 3 to 8 fathoms, mud and rock, or sand; very rare, on *Thyroscyphus vitiensis*.

#### Family LAFOËIDÆ.

##### LAFOËA SERRATA Clarke, 1879.

A widely distributed, but moderately rare species. Repeated regeneration of the hydranth had furnished one hydrotheca (from St. 22) with the exceptionally large number of eleven successive margins.

*Localities.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; fairly common, on *Idia pritis*. St. 9, between Bentinck Island and Courts Island, 12 to 26 fathoms, sand and shell; very rare, on *Thyroscyphus vitiensis*. Stts. 15 and 16, Ravenshaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud; rare, on *Idia pritis*. St. 22, Hastings Harbour, shore to 20 fathoms, rock and sand; fairly common, on *Thyroscyphus vitiensis* and *Idia pritis*. St. 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; rare, on *Eudendrium attenuatum*? St. 25, Gregory Group and Crichton Island, 4 to 14 fathoms, stones and broken shells, and rock; rare, on *Idia pritis*. St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand; rare, on *Idia pritis*.

##### LAFOËA VENUSTA Allman(?), 1877. (Plate LXXVI. figs. 5 & 6.)

Various Hydroids have associated with them a small form which I refer, with a query, to this species.

The trophosome consists of a creeping hydrorhiza from which spring small cylindrical hydrothecæ, set on stout but variable stalks, and zoned by numerous, well-defined, and regular corrugations. These decrease in distinctness towards the base of the hydrotheca. The margin of the hydrotheca is everted, and the stalk bears no regular rings. A marked and distinctive character exists in the colour of the perisarc which possesses a brownish-smoke tint, slightly variable in density. An exceedingly delicate membrane forms the floor of the hydrotheca.

The hydranth is cylindrical and minute, furnished with a hemispherical hypostome, surrounded by tentacles varying in number from nine to eleven. The tentacles and body of the hydranth have a granular appearance owing to the presence of scattered nematocysts, which do not seem, even in the tentacles,

to be arranged in whorls, and of large, deeply stainable cells in the body-wall.

The habit of this epizoon is peculiar, for, in addition to the ordinary external meandering, the cenosarc may live within the perisarcal tube of the hydroid upon which it grows. Thus in several cases, the hydrothecæ of this species project from within the hydrothecæ of *Idia pristis* and *Sertularella quadridens*. In this respect much resemblance is shown to the habit of *Lafoëa dispoliens*, Warren (1909, p. 105), the wanderings of which within the perisarc of its host, *Sertularia bidens* Bale, have been closely traced by Dr. Warren. In the present case, the material being in a poor state of preservation, I have been unable to trace the course of the parasite throughout.

Dimensions :—

Hydrotheca, length.....	0.53-0.84 mm.
„ greatest diameter .....	0.21-0.27 mm.
Peduncle, diameter.....	0.075-0.081 mm.

*Localities.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; solitary hydrothecæ on *Idia pristis* and *Sertularella quadridens*. St. 14, Bushby Island pearling-ground, shore to 21 fathoms, sand and mud; rare, on *Idia pristis*. Stts. 15 and 16, Ravenshaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud; very rare, on *Idia pristis*. St. 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; very rare, on *Sertularella quadridens*.

Hitherto this species has been found only on the western sea-board of the North Atlantic Ocean, and growing upon only one host, *Lytoscyphus marginatus* Allman: Loggerhead Key, 9 fathoms (Allman, 1877), 10 miles north of Zoblos Island (Clarke, 1879), Anguilla, Antilles, 100-150 fathoms (Jüderholm, 1903), off Bermuda, 30 fathoms (Ritchie, 1909 a), and Prof. S. F. Clarke, in *litteris* 1909, mentions its occurrence at West Florida, 20 fathoms, again on *Lytoscyphus marginatus*.

*Systematic position.*—The general appearance of the specimens described as *Lafoëa venusta* resembles that of a small parallel-sided form of the exceedingly variable *Campanularia corrugata* Thornely. As the gonosomes of both species are unknown, and even the hydranth of the former is undescribed, the difficulties of identification are thus greatly increased. The present specimens are, however, specifically distinct from *Campanularia corrugata*, on account of the much smaller size of their hydrothecæ, which are also more regularly ringed, and are always cylindrical in shape. The hydranths also differ in shape and in structure. Those of the present specimens are more slender and possess 9 to 11, in place of 22 tentacles; they have a more hemispherical hypostome, and lack the peculiar development of those endodermal cells, which, in *C. corrugata*, project from the base of the tentacles into the gastric cavity, almost meeting there below the

hypostome, and reminding one of the structure of *Bonneriella grandis*, described by Broch (1909 a, p. 195). I have not noticed that in Miss Thornely's species the perisarc is tinged with brown.

To *Lafœa venusta* I have, with a little doubt, referred my specimens because of the shape, the small size, and the corrugated walls of the hydrothecæ.

### FAMILY SERTULARIDÆ.

SERTULARELLA CYLINDRICA Bale, 1888. Var. PUSILLA, nov.  
(Plate LXXVII. fig. 9.)

Simple stems spring from a creeping stolon, and these are divided into internodes of exceeding variable length by slightly slanting nodes. At the distal end of each internode a hydrotheca is borne.

The hydrothecæ are alternate, and have very thin, collapsable walls, in strong contrast with the thick internodal perisarc. In comparison with the stem upon which they are carried, the hydrothecæ are very large. In shape they are cylindrical, the cylinder expanding slightly at the mouth and forming an everted margin, entire, and destitute of operculum. For about a third of their length they are adnate to the internode, but beyond this their free portion curves gracefully away from the stem, so that the aperture faces upwards and outwards, the plane in which it lies meeting the stem at an angle of about 45°. A slight break in the even abcauline profile of the hydrotheca opposes the point where the adcauline side becomes free from the stem. Often the bottom of the hydrotheca is rounded. Stolons are occasionally developed from the stems, and one was observed springing from the inside of a hydrotheca.

Gonosome unknown.

Dimensions:—

	Var. <i>pusilla</i> .	Typical form.*
Internodes, length .....	0.27-0.36 mm.	very variable.
„ diameter .....	0.06-0.07 mm.	up to 0.39 mm.
Hydrotheca, depth .....	0.29-0.37 mm.	0.80-0.84 mm.
„ diameter at mouth .....	0.10-0.11 mm.	0.32 mm.

*Localities.* St. 32, south-west of Domel Island, 26 to 29 fathoms, sand and mud; rare, on *Lytocarpus phæniceus*. Moskos Islands, 3 to 26 fathoms, rock and sand, or rock and mud; a single stem amongst the rhizoidal tubes of *Idia præstis*.

The species has hitherto been found only on the east coast of Australia, at Port Jackson (Bale, 1888, p. 765).

*Systematic position.*—While I do not find in this form characters sufficient to separate it specifically from *C. cylindrica*, it can readily be distinguished from the Australian form, examples of which I have recently had an opportunity of examining, chiefly

\* Specimens collected off New South Wales by the 'Thetis,' 1898, entrusted to me for examination.

by its dwarfish size—the diameter of the stem is only  $\frac{1}{5}$ , the length of the hydrothecæ less than  $\frac{1}{2}$ , their diameter  $\frac{1}{3}$  those of typical Australian specimens (*cf.* table of dimensions given above). Var. *pusilla* is also to be distinguished by the slightly more flaring margin of its hydrothecæ, and by its hyaline perisarc, for that of the robust typical variety is tinged with brown. It is possible that the discovery of their gonosomes may separate those two forms specifically.

Professor C. Hartlaub, in his fine monograph of the genus *Sertularella* (1900, p. 65), regards *S. cylindrica*, somewhat doubtfully, as a synonym of *S. integra* Allman, described from New Zealand specimens. The delicate texture of the hydrothecæ is so different, however, from that of the type of *Sertularella* which bears intrathecal marginal teeth, that, apart from other obvious differences of form, sculpture, and proportion, I regard the presence of intrathecal teeth in Allman's species as sufficient, in this case, to indicate specific difference.

#### SERTULARELLA POLYZONIAS Linnæus, 1758.

##### Var. CORNUTA Ritchie (?), 1909 b.

A single fragmentary colony, 34 mm. high, represents this species. The hydrothecæ agree in structure with typical specimens, but a single internode occasionally bears more than one hydrotheca. The habit of the colony, too, is much more definite than that of the lax variety (*gracilis*) of British seas, for from a definite, thick stem spring alternate branches almost at right angles. In this respect the specimen approaches var. *robusta* Kirchenpauer (1884, p. 38), from Cape of Good Hope, and var. *cornuta*, from the neighbourhood of the Andaman Islands. The absence of the gonosome precludes certain decision as to which variety it belongs, but the trophosome agrees in detail with that of var. *cornuta*.

##### Dimensions:—

Stem, diameter .....	0.63–0.70 mm.
Hydrotheca, length of adnate portion .	0.32–0.45 mm.
"      "      free      "	0.28–0.39 mm.
"      greatest diameter .....	0.24–0.25 mm.
"      diameter at mouth.....	0.17–0.18 mm.

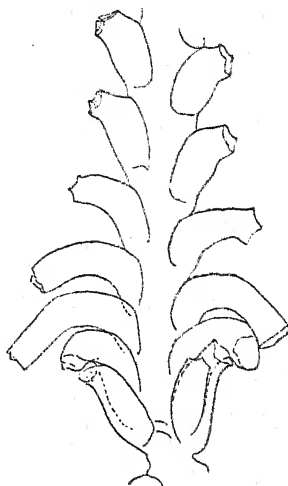
*Locality.* St. 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; rare.

#### SERTULARELLA QUADRIDENS Bale, 1884. (Plate LXXVII. figs. 12 a, 12 b.)

The transverse chitinous projections from the bases of the hydrothecæ are mostly absent, and where they do occur are much less distinctly marked than in Bale's figure (pl. vii. fig. 5) of a Holborn Island specimen. The hydrothecæ are strictly alternate, but the internodes are very irregular in length, from eleven to thirty-six hydrothecæ occurring between successive nodes.

Considerable variation occurs also in the proximity of the hydrothecæ of the same lateral series, for while a marked gap separates some—usually on the distal portions of branches—in many cases the upper portion of one hydrotheca is pressed against the base of the next (*cf.* Pl. LXXVII. figs. 12 *a*, 12 *b*). An abnormality in the formation of the hydrothecæ is worth noting. Occasionally, probably after some accident to the branch, the hydrothecæ first formed thereafter, while normal so far as the adnate portion is concerned, have an exceptionally long portion free (0.77 mm., as contrasted with the average 0.1 mm.), this part being tubular, recurved, and having a rather indefinite margin. Its successor is less, though still abnormally large, and the diminution continues until the normal size is reached after five or six hydrotheca-pairs (text-fig. 79).

Text-fig. 79.



Abnormal hydrothecæ of *Sertularella quadridens*,  $\times 20$ .

The pinnae, each of which arises beneath a hydrotheca, are regularly alternate, three hydrothecæ being interposed between two pinnae on the same side. In one case a branch, of second degree, was observed to spring from the lumen of a hydrotheca.

The structures of the soft parts of the species, to which I have seen no reference, show points of interest. The cœnosarc of the stem is arranged in a varying number of longitudinal strands, usually three or four, which are connected irregularly by anastomosing canals, and which, with their connections, line the perisarc. In the branches the structure is less complicated. There, two large longitudinal cœnosarc tubes are to be distinguished, one running along each side of the branch, and threading its way



between the hydrothecæ. These are connected at the base of each hydrotheca by a strong bridge of cœnosarc, upon the middle of which the base of the hydranth rests. These structures closely resemble those which Nutting has observed in *Selaginopsis ornata* (1904, p. 7), allowing for the differences in symmetry due to the presence of four series of hydrothecæ in that species, in place of two in this. Although each tube possesses a thick definite ectoderm, I have been unable to distinguish the perisarc which, Nutting supposes, surrounds each cœnosarcal tube.

The structure of the polyp is like that of *Thuiaria robusta*, as figured by Nutting (1904, p. 11, fig. 15). It has a large blind sac, and clumps of large endodermal cells project into the hydranth cavity except from the abcauline wall of the blind-sac, where the development of the endoderm is insignificant. The protractor band is attached, not to the abcauline wall of the hydrotheca, but to varying points of the lateral wall in the neighbourhood of the margin of the hydrotheca.

The gonosome was not observed.

Dimensions:—

Stem, diameter .....	0.56-0.77 mm.
Stem internode, length .....	2 mm.
Hydrotheca, length adnate.....	0.46-0.49 mm.
"    "    free .....	0.07-0.14 mm.
"    diameter at mouth .....	0.21-0.22 mm.

*Localities.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; several fragments. St. 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; one colony. St. 25, Gregory Group and Crichton Island, 4 to 14 fathoms, stones and broken shells, and rock; one colony.

Previously known only from Eastern and Northern Australia; Port Curtis and Holborn Island (Bale, 1884), Peel Island, Moreton Bay (Bale, 1888), Flinders Passage, Torres Strait (Allman, 1888, as *Thuiaria vineta*\*), Thursday Island (Weltner, 1900).

#### IDIA PRISTIS Lamouroux, 1816.

One of the commonest of the species in the collection, found at eight of the fourteen stations at which Hydroids were obtained. There is much variability in the length of the free portion of the hydrotheca, the sloping operculum appearing, in some cases, to project directly from the surface of the stem, while in others a large part of the hydrotheca stands out at right angles to the stem. Occasionally, too, the adcauline operculum is lacking in definiteness, the upper wall of the hydrotheca simply meeting the lower as an indefinite flap. Many of the branches from Station 35 end in stolons, indistinguishable from those which project from the hydrorhizal tubes.

\* See Billard, 1908, p. 2 of separate copy.

*Localities.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; common. St. 14, Bushby Island pearling-ground, shore to 21 fathoms, sand and mud; common. Stts. 15 and 16, Ravenshaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud; common. St. 22, Hastings Harbour, shore to 20 fathoms, rock and sand; common, with gonangia, some colonies growing on a sponge. St. 23, Five Islands, 8 to 12 fathoms, rock and sand, and mud; fairly common. St. 25, Gregory Group and Crichton Island, 4 to 14 fathoms, stones and broken shells and rock; common. St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand; one colony. Moskos Islands, 3 to 26 fathoms, rock and sand, or rock and mud; common, with gonangia.

DIPHASIA DIGITALIS Busk, 1852.

In these specimens it is clearly seen that the two so-called opercular muscles are attached, not to the valves of the operculum, but to the lateral walls of the hydrotheca near the margin, and are, in function, protractor muscles (see Nutting, 1904, p. 13, fig. 17). The hydranth possesses about twenty tentacles.

*Locality.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; several small colonies, on the bare axis of an Alcyonarian, and on *Idia pristis*.

Recorded from the Western Indian Ocean—Maldivé Islands—by Borradaile (1905, p. 842); this is the first record from the Eastern Indian Ocean.

SERTULARIA TURBINATA Lamouroux, 1816.

(=*S. loculosa* Busk 1852 \*.)

Several small, unbranched colonies of this species occur upon *Thyroscyphus vitiensis*. They are pale in colour, in this, as well as in the shortness of the internodes, agreeing with the specimens described from Paumben, India, by Jäderholm (1903). But they differ in the reduction of the lateral teeth, which are occasionally so indistinct that the aperture appears to be almost round. Besides an indistinct tooth on each flank, the hydrotheca is surmounted by a small third tooth, from the summit of which a membranaceous edge sometimes runs to the lateral teeth. Notwithstanding difficulties of observation, I feel assured, after examining many hydrothecæ, that the operculum is formed of a solitary flap, hinged on the distal edge of a slight thickening which occurs on the abcauline margin of the hydrotheca. Although membranes unite the superior with the lateral teeth, these do not hinge inwards, and can scarcely, therefore, be accounted part of the operculum. They are the less necessary since the abcauline flap is of diameter sufficient completely to close the aperture of the hydrotheca.

\* *Fide* Billard (1909, p. 322), who has examined the type specimen of Lamouroux.

In the structure of the operculum *S. turbinata* appears to differ from *S. versluysi* Nutting (1904)—regarded by Billard (1908) as a synonym—for in the latter, as Congdon states (1907, p. 482), and as careful examination of the lateral aspect of specimens from Cape Verde Islands, in my collection, shows, the operculum is furnished with a large abcauline and two smaller latero-adeauline valves.

The protractor of the hydranth, which possesses only a small blind-sac, is attached to the hydrothecal wall at the intrathecal ridge.

*Localities.* Stt. 15 and 16, Ravenslaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud; not common.

#### Family PLUMULARIDÆ.

##### PLUMULARIA SETACEA Linnaeus, 1758 (?).

A single immature colony, 15 mm. high, identical in all respects with North Sea specimens. I have written the designation with a mark of interrogation on account of the impossibility of distinguishing the trophosome of this small variety from that of *P. strictocarpa* Pictet (1893), from Amboyna.

*Locality.* Moskos Islands, 3 to 26 fathoms, rock and sand, or rock and mud.

##### PLUMULARIA sp.

An unidentifiable fragment, the structures of the stem and hydroclades of which resemble those of *P. setacea*, but the fragment shows traces of branching, and the hydrotheca of having a slightly concave contour.

*Locality.* St. 32, Hastings Harbour, shore to 20 fathoms, rock and sand.

##### ANTENELLA SECUNDARIA Gmelin, 1788-93.

The nematocysts of the nematophores measure  $12\ \mu$  by  $4\ \mu$ , agreeing with Warren's measurements of those in *A. natalensis*, which I regard as a synonym. There are about 18 tentacles.

*Locality.* St. 1, east of Tavoy Island and Port Owen, 4 to 12 fathoms, sand and broken shells, and mud; not common, on *Idia pristiis*.

##### LYTOCARPUS PENNARIUS Linnaeus, 1758.

A widely distributed species, represented by several fine colonies, one of which reached a height of 95 cm. Apart from the prominent anterior tooth, that on the margin of the hydrotheca second from the stem is distinctly the largest. It forms the highest point on the outwardly curved margin of the hydrotheca. There is, however, some variation in the prominence of

the teeth in general. The margin of the mesial sarcotheca is slightly sinuated.

The attachment of the hydroclades to stem and branches is weak, for, whenever an attempt is made to clear the specimen of flesh, by immersion in a solution of sodium hydrate, the hydroclades invariably fall off.

The soft parts of the specimens from Station 9 are well preserved, as the preservation of Plumularians in general collections goes. The tentacles are about sixteen in number. The whole of the inside of the hydrotheca, practically to the margin, is lined with a thin layer of ectoderm, with which the hydranth is in connection by means of exceedingly numerous strands which, proceeding from its ectodermal layer, give the appearance of filling the space between hydrotheca and hydranth with a delicate open meshwork. An opening leads from the hydrotheca cavity to that of the mesial sarcotheca, immediately proximal to the point where the sarcotheca joins the hydrotheca, and through this passes a strand of *cœnosarc*, connecting *sarcostyle* and hydranth.

A hydrotheca was observed, abnormal in lacking a mesial sarcotheca.

*Localities.* Specimens from Stt. 9, 18, 19, 25 bore phylactocarps. St. 9, between Bentinck Island and Courts Island, 12 to 26 fathoms, sand and shells; one colony. St. 18, west and south-west of Paye Island, 10 to 21 fathoms, sand, shells and rock; a large colony. St. 19, Paye Island and Pink Island, 7 to 9 fathoms, rock and sand; fragment. St. 25, Gregory Group and Orichton Island, 4 to 14 fathoms, stones and broken shells, and rock; three colonies. Moskos Islands, 3 to 26 fathoms, rock and sand, or rock and mud; fragment.

#### LYTOCARPUS PHŒNICEUS Busk, 1852.

The hydrothecæ of these specimens approach most closely those of Bale's fig. 2, pl. xv., 1884, although the chitinous septa and walls are not so strongly developed in my specimens, and the small lobe at the back of the hydrotheca is not produced into a tooth. There are two sarcothecæ at the base of each hydroclade—one proximal, the other lateral—and, in addition, a *sarcostyle* issues through a mere perforation with raised lips, on the anterior of the stem-process on which the hydroclade is borne.

*Localities.* Stt. 15 and 16, Ravenshaw Island, Sir John Malcolm Island, and Alligator Rock, 5 to 18 fathoms, rock and sand, or rock and mud; three colonies. St. 32, south-west of Domel Island, 26 to 29 fathoms, sand and mud; one colony. St. 35, between Warden Island, Howe Island, and Lyall Island, 15 to 20 fathoms, rock and sand; one colony. Moskos Islands, 3 to 26 fathoms, rock and sand, or rock and mud; one colony.

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## EXPLANATION OF THE PLATES.

## PLATE LXXVI.

- Fig. 1. *Corydendrium sessile*, sp. n. Complete colony. About nat. size.
2. " " " Portion of branch with hydranths.  $\times 25$ .
3. *Calyceella oligista*, sp. n. Hydrotheca and hydranth.  $\times 230$ .
4. " " " " " "
5. *Lafôea venusta* Allman (?). Hydrotheca and hydranth.  $\times 60$ .
6. " " " " " "

## PLATE LXXVII.

- Fig. 7. *Thyrosocyphus regularis* Jäderholm. Portion of branch with hydrotheca and gonangium.  $\times 25$ .
8. *Cuspidella costata* Hincks. Hydrotheca, showing character of annular markings.  $\times 70$ .
9. *Sertularella cylindrica*, var. *pusilla*, nov. Portion of stem, with hydrothecæ.  $\times 46$ .
10. *Halecium simplex* Pictet. Trophosome and gonosome.  $\times 70$ .
11. " " " Hydrotheca, showing internal chitinous projections.  $\times 310$ .
12. *Sertularella quadridens* Bale. Showing variation in remoteness of hydrothecæ. (a) Proximal portion of branch. (b) Distal portion of same branch. Each  $\times 19$ .

4. Hydroids from Christmas Island, Indian Ocean, collected by C. W. Andrews, D.Sc., F.R.S., F.Z.S., in 1908. By JAMES RITCHIE, M.A., B.Sc., Natural History Department, The Royal Scottish Museum\*.

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(Text-figures 80 & 81).

The present paper gives account of a small collection of Hydroids which formed part of the Marine Invertebrate collections obtained by Dr. Andrews during the autumn of 1908. The smallness of the collection, however, is hardly to be taken as an indication of the poverty of the Hydroid fauna of the Island, for Dr. Andrews found that, at virtually all points, shore-collecting was dangerous or impossible. The present specimens, therefore, were obtained in a limited area: in Flying Fish Cove, either on the shore, or on a reef laid bare at low tide.

The collection is of interest as being a first sample of the Hydroid fauna of this isolated island; and in spite of its limitation, for it contains representatives of only thirteen species, it adds four of these to the known fauna of the Indian Ocean. The most remarkable of these additions are hydranths which exactly correspond with those of *Rhizogeton nudum*, described by Broch, in 1909, from Spitsbergen.

I have to thank Mr. R. Kirkpatrick, of the British Museum, for giving me the opportunity of examining the collection.

*List of Species.*

**Gymnoblastea.**

Family CLAVIDÆ.

*Rhizogeton nudum* Broch (?)

Family EUDENDRIDÆ.

*Eudendrium parvum* Warren (?)

Family PENNARIDÆ.

*Pennaria disticha* Goldfuss, var. *australis* Bale.

Family TUBULARIDÆ.

*Tubularia crocea* Agassiz.

**Calyptoblastea.**

Family CAMPANULARIDÆ.

*Campanularia corrugata* Thornely.

*Clytia noliformis* M'Crady (?)

*Clytia serrulata* Bale.

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\* Communicated by R. KIRKPATRICK, F.Z.S.

## Family SERTULARIDÆ.

*Sertularella polyzonias* Linn.*Thuiaria tubuliformis* Marktanner.

## Family PLUMULARIDÆ.

*Plumularia buskii* Bale.*Plumularia setacea* Linn. (?)*Plumularia* sp. (*megalocephala* Allman, aff.).*Halicornaria hians* Busk, var. *laxa*, nov.

## NOTES ON THE SPECIMENS.

## GYMNOBLASTEÆ.

## Family CLAVIDÆ.

## RHIZOGETON NUDUM Broch (?)

1909. *Rhizogeton nudum* Broch, Hydroiden, in Fauna Arctica, Jena, vol. v. p. 137, fig. 1.

On the surface of a fragment of millepore there occurred a delicate stolon from which solitary hydranths sprung at intervals. The stolon is branched, forming a loose, irregular network upon the substratum, and it is protected by a very thin layer of perisarc. No perisarc occurs on the hydranths, even at the base. The hydranths are elongated, subcylindrical or spindle-shaped according to the state of contraction. They are armed with long filiform tentacles varying in number from seventeen to twenty-four or twenty-five, and decreasing gradually in size, from the longest which, in extension, surround the hypostome, to short, stumpy individuals at the base. The tentacles are scattered over all but the lower fourth of the hydranth; but except for four oral tentacles which lie almost in one whorl, no definite arrangement could be traced.

The soft parts are well preserved, and in the hydranth a thin ectoderm with flattened cells could be distinguished, lined by endoderm with elongated cells, which project for a short distance into the digestive cavity, and within which, in some hydranths, lie clusters of minute, deep-brown, almost opaque spherules, probably refuse products of digestion. The internal portions of the tentacles are filled by a septate skeletal endoderm. The growing point of the stolon, in the one instance observed, was formed of a thick pad of ectodermal cells, which gradually dwindled into the insignificant layer which lines normal portions of the stolon.

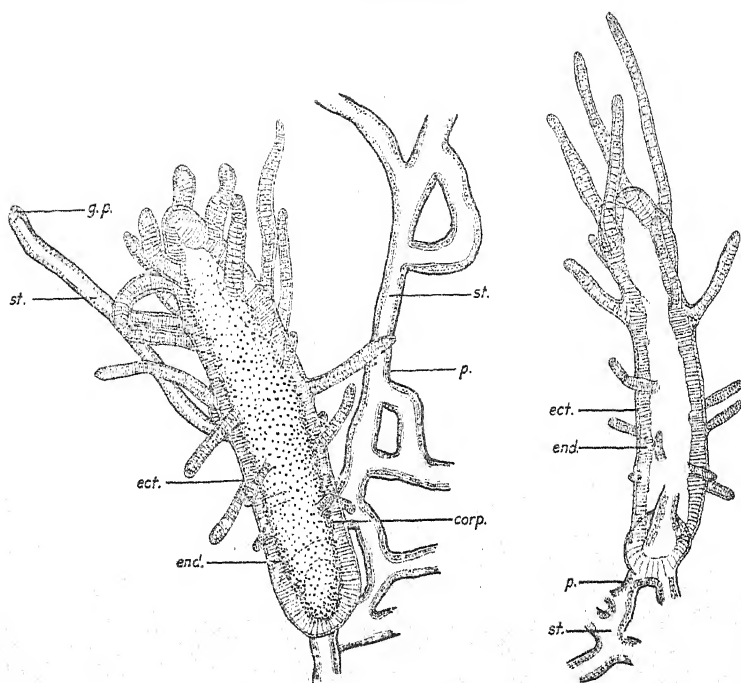
The gonosome was not observed.

Dimensions:—

Stolon, diameter.....	0.060 mm.
Hydranth, length .....	0.77   0.92   to 2 mm.
„ greatest diameter	0.17   0.21   mm.



Text-fig. 80.

*Rhizogeton nudum* (?),  $\times 65$ .

*corp.*, dark corpuscles in endoderm of hydranth; *ect.*, ectoderm; *end.*, endoderm; *g.p.*, growing point of stolon; *p.*, perisarc; *st.*, stolon.

*Locality.* Flying-Fish Cove.

Owing to the absence of the gonosome, identification with *R. nudum* must remain a matter of doubt. The trophosomes, however, agree in shape, in character, and in the number and position of the tentacles; and Broch's figures represent hydranths which agree in size with those from Christmas Island, although he states that his hydranths may attain a length of 4 mm. The original specimens of *R. nudum* were obtained by the 'Helgoland' Expedition, in Bismark Sound, east of West-Spitsbergen, at a depth of 35 metres.

Family EUDENDRIÆ.

EUDENDRIUM PARVUM Warren (?)

1908. *Eudendrium parvum* Warren, Ann. Natal Government Mus. vol. i, pt. 3, p. 272, text-fig. 1, pl. xlv. figs. 1-4.

A single fragment of creeping stolon, from which spring two

simple stems, and one, showing traces of a branch, occurred on the surface of a fragment of millepore. The gonosome is absent, and the characters of the hydranths have all but disappeared, but the perisarc of the trophosome shows the structures described by Warren. The stolon measures  $102\mu$ , and the hydrocauli from  $81\mu$  to  $111\mu$ , in diameter, but the unbranched hydrocauli are very short, less than 2 mm. in height.

*Locality.* Flying-Fish Cove.

#### Family PENNARIIDÆ.

PENNARIA DISTICHA Goldfuss (= *P. carolinii* Ehrenb.), var. AUSTRALIS Bale.

\*1820. *Pennaria disticha* Goldfuss, Handb. der Zool., Nurnberg, p. 89.

1884. *Pennaria australis* Bale, Cat. Australian Hydroid Zooph., Sydney, p. 45.

Several well-preserved colonies of this variety, distinguished from typical *P. disticha* by the restriction of the annulation of the peduncles to six, or fewer, rings at the base, and by the small size of the colonies, were obtained. No gonosome is present, and the specimens are overgrown by seaweed and diatoms.

*Locality.* Flying-Fish Cove.

#### Family TUBULARIDÆ.

TUBULARIA CROCEA Agassiz.

1862. *Paryppha crocea* Agassiz Contr. Nat. Hist. U.S., vol. iv. p. 249.

A considerable number of specimens of a small *Tubularia*, with stems up to 25 mm. high, show the following significant characters. The stems are white, becoming faintly tinged with yellow at the base. They are mostly unbranched, or have a few straggling offshoots at the base, and they are marked here and there by groups of faint annulations. The hydranth is translucent, set above a marked dilatation, the lower part of which is protected by thin, wrinkled perisarc, while on the upper portion the ectoderm is markedly thickened, appearing as if it hung downwards from the base of the hydranth in a short flap. In this respect, and in the separation of the hydranth cavity from that of the dilatation, the structures are similar to those of *T. bethæ* Warren, but the ectoderm of the present specimens is also much thickened at the neck beneath the dilation, and the endoderm lining the dilation does not exhibit the development of elongated cells which Warren describes†.

In these specimens the oral tentacles number about 15 to 17, and the proximal tentacles about 18 to 20, set in single whorls.

\* For synonymy see Bedot, Rev. Suisse de Zool., vol. ix. 1901, p. 459.

† Warren, Ann. Natal Government Mus., vol. i. 1908, p. 282.

The blastostyles are short, generally erect, although some tend to droop through the row of tentacles, and they are closely set with male gonophores, characterised by their elliptical shape, and by the replacement of tentacular rudiments by a single terminal wart. Unfortunately, female gonophores have not been observed. The characters, however, point to identity with *T. crocea*, the male gonophores of which, according to Allman, are "destitute of [tentaculiform] processes," although Torrey's observations show that the presence or absence of tentacular processes is variable\*.

Dimensions:—

Stem, diameter .....	0.31 mm.
Hydranth, height (from base of dilation)...	about 3 mm.
"    diameter at level of proximal tentacles .....	about 2 mm.

*Locality.* Reef, Flying-Fish Cove.

*T. crocea* has been found on the Atlantic (Agassiz) and Pacific (Torrey) coasts of North America, and in Plymouth Harbour on a ship from Peru (Browne). Specimens were obtained growing amongst barnacles on the screw-casing of the German Antarctic Expedition ship 'Gauss,' while it was in the South Atlantic, and Vanhöffen is of opinion that the specimens settled on the ship during its passage through the south of the Indian Ocean†, in which, until the present record, the species had not been observed.

### CALYPTOBLASTEÆ.

#### Family CAMPANULARIDÆ.

##### CAMPANULARIA CORRUGATA Thornely.

1904. *Campanularia corrugata* Thornely, in Herdman, Ceylon Pearl Fisheries, Part ii. p. 114, pl. i., fig. 2, Suppl. Rep. viii. Hydroids.

A couple of hydrothecæ were observed on *Plumularia buskii* Bale.

*Locality.* Flying-Fish Cove.

##### CLYTIA NOLIFORMIS M'Crady (?).

1876. *Campanularia noliformis* M'Crady, Proc. Elliott Soc. vol. i. p. 194.

A few hydrothecæ, referred to this species, were growing upon a fragment of sponge, and on *Pennaria disticha*, var. *australis*. The hydranths bear twenty tentacles. Without the presence of the gonangia the identification of this species is uncertain, owing to the resemblance of the trophosome to that of *Clytia johnstoni*,

\* Torrey, Univ. California Pub., Zool., vol. i. p. 44.

† Vanhöffen, Deutsche Südpolar-Exp. 1901-1903, vol. xi. Zool. iii. Berlin 1909: die Hydroiden, p. 279.

but I have been guided by the very small dimensions of these specimens, which are even less than those of specimens recorded by Pietet from Amboyna\*, and by Vanhöffen from the South Atlantic†, and approach most closely in size the original specimens of *Campanularia attenuata* Calkins, regarded by Vanhöffen (l. c.) as identical with *Clytia noliformis*.

Dimensions :—

Total length .....	1·5–2·5 mm.
Stem, diameter .....	0·054–0·066 mm.
Hydrotheca, depth.....	0·32–0·45 mm.
"    diameter at mouth .....	0·21–0·28 mm.

*Locality.* Flying-Fish Cove.

This species has not hitherto been recorded from the Indian Ocean.

*CLYTIA SERRULATA* Bale.

1888. *Campanularia* ? *serrulata* Bale, Proc. Linn. Soc. N. S. Wales (2), vol. iii. p. 757, pl. xii. fig. 4.

A single poor colony, growing along with *Plumularia setacea* Linn., the structures and dimensions of which agree with those given by authors.

*Locality.* Flying-Fish Cove.

This species has not hitherto been recorded from the Indian Ocean, although Vanhöffen has recently described specimens from Observatory Bay, Kerguelen‡.

#### FAMILY SERTULARIDÆ.

*SERTULARELLA POLYZONIAS* Linn.

1758. *Sertularia polyzonias* Linnaeus, Syst. Nat., ed. x. p. 813.

A solitary colony was found on the stem of *Pennaria disticha*, var. *australis*. Although its structures appear to be indistinguishable from those of *S. polyzonias*, this specimen is exceedingly minute, only 3 mm. high, reminding one of the small New Zealand variety figured by Hilgendorf§; and the dimensions of the hydrothecæ are also very much smaller than those of typical specimens. The hydranth has about twelve tentacles.

Dimensions :—

Internode, length .....	0·28–0·35 mm
"    diameter .....	0·08 mm.
Hydrotheca, length .....	0·28–0·31 mm
"    length free .....	0·16–0·18 mm.
"    diameter at mouth .....	0·13 mm.

*Locality.* Flying-Fish Cove.

\* Pietet, Rev. Suisse de Zool., vol. i. 1893, p. 31.

† Vanhöffen, op. cit. p. 299.

‡ Vanhöffen, op. cit. p. 302.

§ Hilgendorf, Trans. New Zeal. Inst. vol. xxx. 1898, pl. xv. fig. 2a.

## THUIARIA TUBULIFORMIS Marktanner.

1890. *Dynamena tubuliformis* Marktanner—Turneretscher, Ann. k.k. Hofmus. Wien, vol. v. p. 238, pl. iv. fig. 10.

Only a few colonies of this species, the largest 15 mm. high, were found. The structures are typical, and agree more closely with Marktanner's and with Nutting's\* figures than with those of Natal specimens by Warren†, in which the hydrothecæ are shown to be less crowded, and are more seldom arranged in groups of several pairs. Our specimens show all the peculiarities of arrangement of hydrothecæ on the stem internodes which Marktanner cites. Most commonly, as in Nutting's specimens, each stem-internode bears "a branch and two hydrothecæ on one side and a single hydrotheca on the other," but occasionally, as Clarke‡ also has found, a hydrotheca-pair is added to this typical internode, and occasionally a hydrotheca-pair is subtracted and isolated on a separate internode, leaving one hydrotheca with its associated branch-process alone on an internode.

## Dimensions:—

Length of colony .....	up to 15 mm.
Typical stem internode, length .....	1.06 mm.
Stem internode, diameter .....	0.18-0.31 mm.
Branch, length .....	about 5 mm.
Hydrotheca, length of adnate portion.....	0.42 mm.
" " free " .....	0.11-0.15 mm.
" diameter .....	0.14 mm.

*Locality.* Reef, Flying-Fish Cove.

This species has now been found in the Eastern Pacific Ocean (Perico Island, Gulf of Panama—Clarke, 1907); in the Western Atlantic Ocean (Bahia; Florida; Bahama Banks—Nutting, 1904); in the Eastern Atlantic Ocean (St. Thomas Island—Billard, 1907); in the Red Sea (Jidda—Marktanner, 1890; Suez Bay—Thornely, 1908); from the West Indian Ocean (Natal—Warren, 1908); and now from the East Indian Ocean. Pictet has recorded from Amboyna, in the East Indies, specimens which he has named *Sertularia vegæ* (Thompson), as a synonym of which he ranks *Dynamena tubuliformis* Marktanner§. With Jäderholm||, I am of opinion that these specimens are not to be identified with *T. vegæ*. They clearly belong to *T. tubuliformis*.

## Family PLUMULARIDÆ.

## PLUMULARIA BUSKII Bale.

1884. *Plumularia buskii* Bale, Cat. Australian Hydroid Zooph., Sydney, p. 124, pl. x. fig. 3, pl. xix. figs. 34, 35.

Several colonies occurred growing on a sponge. They are much

\* Nutting, "American Hydroids," Spec. Bull. Smiths. Inst., Part 2, 1904, pl. xi. figs. 1, 2, 3.

† Warren, op. cit. p. 315, text-fig. 12.

‡ Clarke, Mem. Mus. Comp. Zool. Harvard, vol. xxxv. 1907, p. 14.

§ Pictet, Rev. Suisse de Zool. vol. i. 1893, p. 44.

|| Jäderholm, Kungl. Svenska Vet.-Ak. Händl. vol. xlv. 1900, p. 91.

smaller than the two or three inch high specimens described by Bale, and even than Miss Thornely's immature Ceylon examples; for the largest is under 15 mm. in height. On account of the absence of intermediate athecate internodes from the hydrocaulus, and of the presence of a minute median nematophore, with small and delicate pedunculate sarcotheca, in the angle behind the hydrotheca, the species can readily be distinguished from the very similar *P. cornucopie* Hincks, and *P. alternata* Nutting. Hartlaub\* has described a specimen from Laysan, in which the minute sarcotheca immediately behind the hydrotheca is assuredly absent, and which, notwithstanding, he assigns to *P. buskii*; but I regard the specific identity of the two forms as doubtful.

The following observations supplement Bale's description. The lower portion of the stem consists of a varying number of nodes separated by transverse joints, the lower nodes being altogether destitute of appendages, while those nearest the cladate portion of the stem, from which they are separated by an oblique node, bear a series of several sarcothecæ. The hydroclades spring alternately from one side or the other of a hydrotheca. In rare cases, opposite hydroclades arise from the proximal cladate internode, as in Miss Thornely's specimens. The hydroclades rest on a very insignificant process of the internode, which coincides with the base of the lateral nematophore. A strong constriction separates this stem-process from the hydroclade, although these specimens do not show the excessive tendency to deciduousness of pinnae which Bale noted.

At the origin of the hydroclades there are generally two very short internodes (although rarely only one is present) without appendages, and with transverse nodes; and these are succeeded by a longer internode which bears, on its anterior surface, a single pedunculate sarcotheca on a swelling near its proximal end, and is limited by a proximal transverse node, and by a distal oblique node which separates it from the first thecate internode. In these specimens the hydroclade is very distinctly divided, by transverse and oblique joints, into intermediate internodes furnished with a single nematophore, and hydrothecate internodes; and although Bale describes "a hydrotheca on each, except the first [internode] of each pinna," his figure (pl. x. fig. 3) indicates the presence of an obscure horizontal constriction immediately above the hydrotheca. Only very exceptionally does the fusion of an intermediate with the preceding hydrothecate internode occur in these hydroclades, a phenomenon recorded by Billard in the lower portion of the hydrocaulus of the closely related *P. cornucopie*†.

While emphasizing the fixedness of the median sarcothecæ in his original description, Bale later regarded only the sarcotheca beneath the hydrotheca as fixed‡. I am inclined to agree with the earlier statement, as the large area of their attachment, and

\* Hartlaub, Zool. Jahrb. Syst., vol. xiv. 1901, p. 374, pl. xxi. figs. 22, 32, 36.

† Billard, Exp. Sc. 'Travailleur' et 'Talisman,' vol. vii. 1907, p. 207.

‡ Bale, Trans. Roy. Soc. Victoria, vol. xxii. 1886, p. 94.

the invariable position they assume, seem to show that there is no movability in any of the median sarcotheca.

The colonies are mature, male gonangia arising from the stem at the proximo-lateral portion of a hydrotheca, on the side other than that from which a hydroclade springs. They are club-shaped in lateral aspect, resembling the gonangia of *P. geminata* Alblun, and are furnished with a stalk consisting of two short internodes, each of which has a thick adcauline wall, from which, in the second, a diminutive chitinous ledge projects inwards. Although a nematophore usually occurs on each side of the gonangium, occasionally only one side is furnished with an individual.

Dimensions :—

Stem internode, length .....	0.35–0.43 mm.
diameter .....	0.07–0.11 mm.
Hydroclade, length .....	up to 2 mm.
"          thecate internodes, length *.....	0.25–0.34 mm.
"          intermediate "          "          .....	0.18–0.21 mm.
Hydrotheca, depth .....	0.21–0.22 mm.
diameter at mouth .....	0.17–0.18 mm.
Gonangium (male), length.....	0.36–0.42 mm.
"          "          greatest diameter in lateral aspect .....	0.17–0.18 mm.

*Locality.* Growing on a sponge from the Reef, Flying-Fish Cove.

The only previous Indian Ocean record is that of Miss Thornely, from Gulf of Manaar.

#### PLUMULARIA SETACEA Linn. (?).

1758. *Sertularia setacea* Linnæus, Syst. Nat. p. 813.

Many small colonies apparently belonging to this widely-distributed species, and averaging 15 mm. in height, were found growing on a sponge. As it seems impossible to separate this species from *P. strictocarpa* Pictet by characters of the trophosome alone, and as the gonosome is not present on any of these specimens, I refer them doubtfully, by courtesy, to the older, and cosmopolitan species, until the discovery of the gonotheca shall fix their identity. For guidance I append dimensions of parts.

Stem internode, length.....	0.31–0.49 mm.
diameter.....	0.051–0.159 mm.
Hydroclade, length .....	2–3 mm.
Hydrothecate internode, length .....	0.32–0.36 mm.
Intermediate "          "          .....	0.17–0.25 mm.
Hydrotheca, depth .....	0.090 mm.
diameter at mouth .....	0.096–0.105 mm.

*Locality.* Reef and piles of the pier, Flying-Fish Cove.

\* Measured from extreme points.

*PLUMULARIA* sp. (*megalocephala* Allman, aff.).

Growing on the base of a stem of *Halicornaria hians*, var. *laxa*, were two simple stems of a *Plumularia* which remains unidentified. Most of the hydroclades have disappeared, but sufficient remains to show that the trophosome is akin in structure and relative proportions to that of *P. megalocephala* Allman, found on the shores of the western Atlantic and eastern Pacific Oceans. From this they appear to differ only in their simple habit and small size, and in lacking that sarcotheca which occurs on the stem internodes, immediately proximal to the hydroclade-bearing process.

## Dimensions:—

Stem, length .....	9 mm.
Stem internode, length .....	0.35–0.49 mm.
"    "    diameter .....	0.039–0.084 mm.
Hydrothecate internode, length .....	0.31 mm.
"    "    "    diameter .....	0.019–0.027 mm.
Basal athecate internode, length .....	0.14–0.19 mm.
Hydrotheca, depth .....	0.045 mm.
"    diameter at mouth .....	0.048–0.051 mm.

*Locality.* Flying Fish Cove, 46 fathoms.

*HALICORNARIA HIANs* Busk, var. *LAXA*, nov.

This is the species most abundantly represented in the collection. The largest colony is 12 cm. in height, and the minute characters of the hydrotheca agree closely with Bale's \* diagnosis, except that the mesial sarcotheca, in overtopping the hydrotheca-wall for some distance, approaches the condition of that described by Stechow †. The ultimate portion lies, however, at a slight angle to the course of the main portion of the sarcotheca.

There are differences in habit, however, which distinguish this variety. The colonies are delicate and fine in appearance; and the stem is thin and shows no traces of nodal constrictions. The hydroclades, which are of the unusual length of 22 mm. (twice as long as those recorded by Stechow), are alternate, and are wide apart, a space of 2 mm. separating successive individuals on the same side of the stem. They are divided into long internodes, on the upper portion of which the hydrothecae are set. In this respect, and on account of the greater depth (as compared with Bale's and Stechow's figures), and more erect posture of the hydrothecae (the axes of which are inclined to that of the hydroclade at an angle of about 40°, instead of 55°), and of the greater elevation of the intrathecal septum above the floor of the hydrotheca, these specimens resemble var. *profunda*, from the Andamans ‡.

\* Bale, Cat. Australian Hydroid Zooph., 1884, p. 179.

† Stechow, Abh. K. Bayer. Akad. Wissens., Suppl.-vol. i. 3, 1900, p. 101, pl. vi. fig. 16.

‡ Ann. Mag. Nat. Hist. (8) vol. iii. 1900, p. 528.





June 14, 1910.

Dr. S. F. HARMER, M.A., F.R.S., Vice-President,  
in the Chair.

The Secretary read the following report on the additions made to the Society's Menagerie during the month of May 1910:—

The registered additions to the Society's Menagerie during the month of May were 130 in number. Of these 80 were acquired by presentation, 13 by purchase, 23 were received on deposit, 3 in exchange, and 11 were born in the Gardens.

The total number of departures during the month, by death and by removals, was 156.

Amongst the additions special attention may be called to the following:—

One Leopard Cat (*Felis bengalensis*) and one Masked Palm-Civet (*Paradoxurus larvatus*), from Szechuen, China, presented by W. Thurlow-Lay, Esq., on May 23rd.

Two Hunting-dogs (*Lycan pictus*), from Nairobi, presented by H. H. Heatley, Esq., on May 23rd.

One Caracal (*Felis caracal*) ♂, one Chapman's Zebra (*Equus chapmani*) ♂, and two Selous's Marsh-Buck (*Limnotragus selousi*), from Lake Ngami, purchased on May 7th.

One Sabre-horned Oryx (*Oryx algazel*), from Northern Nigeria, presented by Sir Hesketh Bell, on May 8th.

Two Ludwig's Bustards (*Otis ludwigi*) and two Vigors's Bustards (*Otis vigorsii*), new to the Collection, from S. Africa, presented by Sir Charles B. Elliott, K.C.M.G., on May 14th.

Two Manchurian Cranes (*Grus japonensis*), from N. China, purchased on May 23rd.

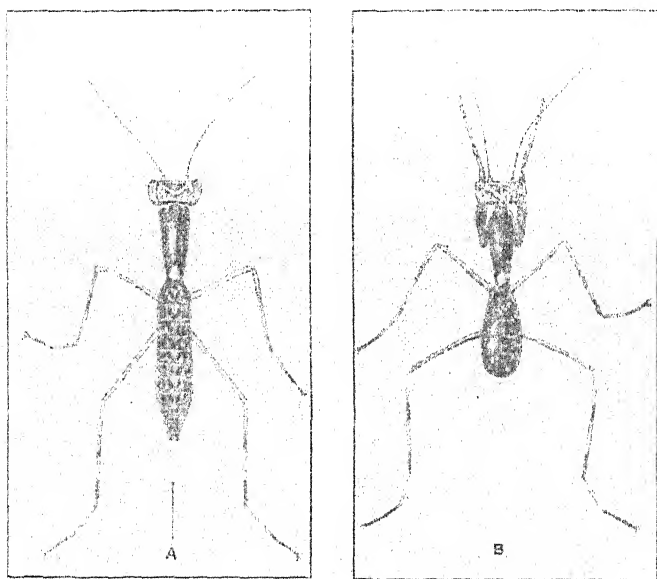
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Mr. R. I. Pocock, F.L.S., F.Z.S., Superintendent of the Gardens, exhibited two drawings (text-fig. 82) illustrating an instance of ant-mimicry by the larvæ of a species of Mantis, and remarked:—

“In May of this year Mr. W. H. Boyle sent to the Society's Gardens, from Axim on the Gold Coast, the nest of a species of Mantis. The nest was about the size of a walnut but less regularly shaped, and pale emerald-green in colour, with a glistening sugary appearance. The day after it was placed in the Insect House, the young insects emerged. They were 4 mm. or less in length, and when crawling about the case looked exactly like a crowd of black ants, their rapid darts and pauses recalling irresistibly the busy method of progression so characteristic of these Hymenoptera. When at rest they no longer resembled the models they imitated when in motion, but assumed the attitude of adult Mantises watching for prey, raising the fore part of the body and head, folding up their fore legs, and every now and then swaying gently from side to side as if rocked by the wind. While thus employed, they were seen to be procryptically coloured. The long

filiform antennae were too delicate to be seen; the large head was mottled pale drab and brown; the long pronotum, which was somewhat abruptly constricted behind the head and gradually narrowed posteriorly, was uniformly black except for a pale whitish spot upon its hinder end; the mesonotal, metanotal, and abdominal terga were, like the head, pale drab relieved by symmetrically arranged brown spots. The effect of the contrast between the prothorax and the head in front of it and of the tergal plates behind it was disruptive, the colour-continuity of the upper surface being destroyed. The fore legs, folded beneath the prothorax, were indistinguishable, and the remaining two pairs

Text-fig. 82.



A. Larva of West African Mantis in resting attitude.

B. The same when crawling, with the fore legs extended and abdomen turned up.

of legs which supported the body were rendered invisible by their greenish coloration matching the green of the leaves. These legs, however, were not of the same tint throughout; the base of the femur was paler than the distal end; the tibia was marked with a median and a distal dark ring, and the end of the tarsus was darker than its proximal portion. The optical effect of this alternate banding with dark and light of the distal half of the legs was discontinuity of surface, the light areas being obliterated against a light background and the dark areas against a dark

background. The whole of the underside of the body was black; the legs of the anterior pair were also mostly black, except for pale annulations on the tibia and tarsus. Two factors were in the main concerned in effecting the likeness to an ant, namely, the blackness of the underside of the abdomen, and the habit of the Mantis, when in motion, of curling the posterior half of the abdomen up like a Scorpion's tail. It resulted from this action that the abdomen was in appearance reduced to about half its real length, its shape being altered to an elongated oval, and since its anal end was brought as far forwards as the posterior extremity of the prothorax, completely covering the metanotal and mesonotal terga, the black of its underside formed with the black of the prothorax a continuous field only broken by the white spot on the prothorax, which, being situated at the narrowest part of the body, exactly simulated an ant's waist. The long and powerful fore legs were extended forwards in crawling, their annulated distal ends projecting some distance in front of the head on each side, so as to resemble the waving antennæ of an ant.

"The above described coloration persisted until the Mantises had attained a length of about 7 mm. At the next moult a remarkable change took place, the prothorax losing entirely its black colour, and with its loss the resemblance to the ants disappeared.

"An apparently similar case of ant-mimicry by the larva of an Indian species of Mantis has been described by de Nicéville in a letter to Prof. Poulton (*see* Shelford, P. Z. S. 1902, vol. ii. pt. 2, p. 232). The Mantises were said to be remarkably like a small black ant; the deceptive resemblance was so close that careful scrutiny was necessary to distinguish the true character of the insects. Although de Nicéville gave no particulars as to the way in which the mimicry was achieved, he noticed that the young Mantises were incessantly moving, just like the ants they mimicked but quite unlike the adults of their own kind. Shelford also recorded an instance observed by himself at Kuchong of mimicry between a Harpagid Mantid (*Hymenopus bicornis*) and a young larva of a distasteful Reduviid bug (*Eulyes amena*)."

[Additional note, added June 15th, 1910, on the mimicry of the larva of the Ceylonese Leaf-Insect (*Phyllium* sp.?).—Dr. A. Willey, F.R.S., on his return from Ceylon, brought a number of eggs of this insect as a present to the Society. The young upon hatching were seen to differ remarkably in colour from the adults. The head, thorax, and anterior part of the abdomen were crimson, the posterior part of the abdomen being much darker and browner in hue and the legs black. The crimson and black coloration made these insects extremely conspicuous on green leaves, and their general appearance was remarkably 'bug'-like. Their scheme of coloration fitted unmistakably into that depicted and described by Shelford (P. Z. S. 1902, vol. ii. pt. 2, pl. xxiii. figs. 1, 2, 3) as illustrated by two species of bugs (*Ectatops rubiaceus*

and *Serinetha abdominalis*), both probably distasteful, and a moth (*Phaula limbata*), all of which mimic a distasteful Lycid beetle (*Lycostomus gestroi*). The resemblance was so close as to leave no room for doubt that similar if not identical species of Lycidae and Hemiptera were mimicked in Ceylon by the larvæ of the *Phyllium*. In the matter of coloration the larvæ of this Ceylon species of *Phyllium* differed markedly from those of the Seychelles species, the only other Leaf-Insect that had been exhibited in the Gardens. In the Seychelles species the young upon hatching were always green like their parents and procryptically coloured.]

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The following papers were read :—

1. On the Specialised Cutaneous Glands of Ruminants.  
By R. I. Pocock, F.L.S., F.Z.S., Superintendent of the  
Zoological Society's Gardens.

[Received June 14, 1910.]

(Text-figures 83-142.)

#### Part I.—INTRODUCTION.

In the 'Proceedings' of our Society for 1836 there is much and varied information, some of it true and some of it false, about the specialised cutaneous glands of Ruminant Ungulates. On pp. 37-38 will be found a table compiled by Owen\* showing the presence or absence of preorbital and inguinal glands in some sixty species of Antelopes. Bennett contributed a note on pp. 34-36 on the preorbital gland of *Antilope cervicapra*; and this was supplemented by remarks from Ogilby on the same gland in this species and in an unidentified species of Gazelle. Bennett also communicated (p. 39) a letter from Hodgson on the inguinal glands of *Pantholops* and on the preorbital glands of *Cervus aristotelis* and of *Capricornis thar*. The subject was further discussed by Ogilby (pp. 131-139) in a paper dealing with the preorbital, inguinal, and pedal glands, and other external features in genera of the families Camelidae, Giraffidae, Cervidae, Antilocapridae, and Bovidae. Finally (on pp. 66-68), Gray described the tarsal and metatarsal tufts of various species of Cervidae.

Eleven years later Hodgson (J. A. S. Bengal, xvi. pt. ii. pp. 685-711, 1847) published a long paper on the same subject, based mainly, but not solely, upon Indian genera of Cervidae and Bovidae, without apparently being aware of the work already done by Owen and Ogilby; and in 1868 Owen reprinted, with slight modifications, his original paper, but without incorporating

\* Apparently largely from data supplied by Hamilton Smith in vol. vii. of Griffith's 'Animal Kingdom,' 1827.

in it the facts established by Ogilby and Hodgson ('Anatomy of Vertebrates,' iii. pp. 632-638, 1868).

These papers contain by no means the first records of the occurrence of specialised integumentary glands in Ruminants; but those of Owen, Ogilby, and Hodgson are apparently the earliest which attempt to deal comprehensively with the subject from the systematic standpoint; they are also important from the conclusion to be inferred from internal evidence, that they are the main source whence English writers of text-books and monographs have borrowed most of the statements regarding these glands. This is a point, however, on which it is impossible to speak with certainty, because of the reticence of the writers regarding their authority for the information they publish. Even so careful and conscientious a zoologist as Blanford\* did not say whether his statements concerning the glands of Indian Ruminants were taken from Ogilby and Hodgson or were based upon his own observations upon new material which he assuredly had the opportunity of collecting in India. The information he gave, however, tallies so closely with that of Hodgson that it is impossible to doubt his great indebtedness to that author.

I think it probable that Messrs. Sclater & Thomas† and Mr. Lydekker‡ depended mostly upon the publications of Ogilby, Hodgson, Blanford, Brooke, and Gray, and upon a few special memoirs by authors like Flower, Garrod, and Forbes, supplemented, no doubt in some cases, by their own observations upon the glands as exhibited by dried or mounted skins. It does not appear, however, that their works contain many new contributions to the subject. The same may be said of Mr. W. L. Sclater's treatise on the Bovidae of S. Africa§, except that the alleged details respecting the preorbital glands of the Tragelaphinae seem to be new, the general statement as to their presence and size having been taken, I infer, from Flower and Lydekker's volume of Mammalia, a standard source of information on this and other subjects since its publication in 1891.

In the above-quoted works will be found many discrepancies and contradictions with regard to the occurrence in particular genera and species of the glands forming the subject-matter of the present paper. These contradictions are difficult to understand, unless the errors be attributable to the examination of defective material. Unfortunately, most authors, like Owen, Ogilby, and Hodgson, are silent as to the nature of the material upon which their observations were made. This omission is important, because inguinal and preorbital glands, obvious enough on fresh skins, may be cut away or otherwise obliterated in the process of

\* 'Fauna of British India: Mammalia.'

† 'The Book of Antelopes,' vols. i. to vi. 1894-1900: R. H. Porter, London.

‡ 'The Deer of all Lands,' 1898; 'Wild Oxen, Sheep, and Goats of all Lands,' 1898; 'Great and Small Game of Europe, Western and Northern Asia, and America,' 1901; 'The Game Animals of India,' 1907; 'The Game Animals of Africa,' 1908: Rowland Ward, London.

§ 'The Fauna of South Africa: Mammalia,' i. pp. 123-258, 1900.

preservation or mounting; and inferences as to the absence or size of preorbital glands based upon the depressions on the lacrymal bone may be quite false.

On account of their conspicuousness, more information about the preorbital glands has been accumulated than about the inguinal or pedal glands. Although statements as to the presence or absence of inguinal glands are not infrequent, very little has been recorded as to their number, depth, and nearness to the mammae. The pedal glands have been described as large or small, deep or shallow, present or absent, but no correct conception of their variability in shape, size, and position is conveyed by published descriptions. The available information, indeed, on such points is so meagre as compared with the number of species in which they have been recorded, that it has not been possible for systematists to use these glands on a large scale for taxonomic purposes.

Apart from the, comparatively speaking, comprehensive works above quoted, there are many isolated memoirs on the glands of particular species. These are quoted in their appropriate places in the text that follows. There is also a considerable literature dealing with the physiology and histology of the glands. The two papers that I have especially consulted are the following:—An important memoir by Max Weber\* upon the structure of the preorbital glands and the nature and use of their secretions in several "Antelopes," with which is incorporated a list of the principal memoirs dealing with the subject of the cephalic glands in this group; and a special treatise by Max Tempel†, which has for its subject-matter the pedal glands mostly of European species of Artiodactyla. This treatise gives a brief summary of the observations of many authors upon the specialised cutaneous glands of this group, as well as of other Mammalia. Max Tempel adds a tolerably complete bibliography of the subject, and describes fully the microscopical structure of the pedal glands of the twelve species examined by him.

In the hopes of adjusting some of the discrepancies above alluded to, of filling certain obvious gaps in our knowledge, and of discovering possibly at the same time new and useful characters for distinguishing genera and classifying higher groups, I began about three years ago, with the sympathetic concurrence of Mr. F. E. Beddard, F.R.S., the Society's Prosector, to dissect, draw, and describe the cutaneous glands of Ruminants that died in the Gardens. But so many important species were unrepresented in our collection, and were likely to remain so, that I soon perceived the necessity of procuring material elsewhere if the work was to

\* Arch. mikr. Anat. xxxi. pp. 500-540, 1888.

† 'Vergl. Anat.-physiol. Untersuch. über die Drüsen der zwischen Klauenhaut der Paarzeher,' Inaug.-Diss., Leipzig, 1896 (pp. 1-67, 12 pls.). I was unable to see a copy of this paper until my own observations upon the same animals were completed. Except in one or two matters of detail, due perhaps to difference of preservation of material, my results were completely in accord with this author's. I am indebted to Mr. B. B. Woodward for the information that a probable abridgment of Max Tempel's paper was published in Arch. Thierheilk. xxiii. pp. 1-48.

be made comprehensive in its scope. I therefore applied to Mr. Rowland Ward, F.Z.S., and to Mr. Edward Gerrard for skins, feet, or masks of specimens that might be discarded in their stores as useless duplicates. To the generous response my appeal elicited, I owe the opportunity of examining these glands in many species I could not otherwise have seen; and I gladly take this opportunity of expressing my indebtedness to Mr. Rowland Ward, to his manager, Mr. J. B. Burlace, and to Mr. Gerrard for the kind help they afforded me. I also applied to Mr. Herbert Bolton, F.R.S.E., F.Z.S., the Curator of the Bristol Museum, for the use of discarded stuffed specimens, and with the sanction of the Committee of the Museum he kindly sent me from time to time material which has been of great use for my work. Finally, I have to thank Mr. Oldfield Thomas, F.R.S., for allowing me free access to the collection of skins under his charge at the Natural History Museum, when I wished to examine representatives of species I had no chance of seeing elsewhere.

But apart from the verification of previously observed facts, very little satisfactory work can be done upon dried skins if left intact. It is true that the absence of glands can in many cases be inferred by superficial scrutiny; but their structure, when they are present, cannot be ascertained without maceration and dissection. It was here that the use of the material lent or given to me by Messrs. Rowland Ward and Gerrard came in. I found that softening the feet or the preorbital glands, when preserved, and cutting them with a razor or sharp knife, revealed surprisingly well the main features of the glands, especially those of the feet, due allowance being made for shrinkage when, as was too commonly the case, the back of the pasterns had been opened and the connective tissue that normally holds the gland in place had been cut away.

In no case did I attempt to ascertain the microscopical structure of the glands themselves, this aspect of the subject having been already worked out by Max Weber, Tempel, and other authors.

On the fresh specimens I generally made a practice of recording and describing the scent of the secretions—that is to say, of comparing the smell to that of other and familiar objects whenever the one reminded me of the other. In some cases this was a simple task. There was, for instance, no mistaking the resemblance between the scent of the secretion of the inguinal glands of *Ovis vignei* and of *Gazella subgutturosa* to the urine of *Mus musculus*, nor of that of the pedal glands of *Lama* to the same substance. But in other cases no such comparison was possible, owing to the fact that the scents were *sui generis* and were therefore not comparable to any substance known to me.

I noted incidentally in most cases the number of mammæ, but I was disappointed in the hope of getting useful taxonomic features from these organs. The typical number in the Ruminants is two pairs, although the occasional presence of three pairs in domestic cattle suggests that six may have been the original total. Two



pairs, however, seem to be invariable in the true Cervidæ; nevertheless, *Moschas*, sometimes at all events, has only a single pair, and two pairs are found in the majority of the Bovidæ. In the Caprinæ and Antilopinæ, however, only a single pair is, as a rule, found, and these represent the posterior pair of the quadrumanate genera; but in Sheep, Goats, and Gazelles the mammæ of the anterior pair are so commonly retained in a vestigial state that it is only possible to affirm of these genera that they usually have but a single pair of mammæ.

I found, on the contrary, as I anticipated, that the glands, and especially the pedal glands, sometimes supplied valuable confirmatory evidence of kinship between genera already affiliated for other reasons, and sometimes showed greater divergence between genera than was previously suspected to exist. But neither the presence nor the absence of the glands could be considered as furnishing in itself evidence of kinship, without other characters being taken into account, because it was clear that the glands had been independently suppressed in genera belonging to different groups.

While working at the pedal glands I was greatly impressed by the difference in the structure of the feet with respect to the encroachment of the "web," or junctional integument, of the digits over the interdigital area, and to the manner in which it is folded. In the case of dried skins it is generally impossible to substantiate the presence of glandular layers; but the interdigital clefts which result from the folding of the integument of the pastern can always be detected whether they be specially glandular or not. It must be remembered, however, that, strictly speaking, glands are never absent, since the skin is furnished with sebaceous and sweat glands which form the basis of the specialised glands here described. The statement that glands are absent merely means that macroscopic inspection fails to reveal evidence of a specialised area of glandular activity or of a particular receptacle for the storage of secretions.

The terminology of the glands and of other features employed in this paper is as follows:—

*Foot*: the terminal portion of the leg between the carpo-metacarpal or tarso-metatarsal joint and the apex of the hoof.

*Fetlock*: the carpo-metacarpal or tarso-metatarsal joint.

*Pastern*: the area between the fetlock and the hoofs.

*Hoof*: the terminal portion of the foot, consisting of the pair of distal phalanges, each of which is covered with naked skin which is softer close to the pastern than distally, where it is protected in front and laterally by the *nail*; the supporting area of the hoof is composed of the *sole* in front and the *heel* behind; the *heel-tie* is the integument which joins the heels together; and the *interungual integument* is the skin that extends forwards from the heels to the front of the pastern above the hoof.

*Pedal glands* are the larger or smaller pocket-like or flask-like invaginations of the skin which open upon the front of the

pasterns or between the base of the hoofs (= postdigital, interdigital, and interungulate glands of Owen; fossæ interdigitales of Ogilby; interdigital pits of Hodgson; foot-glands or hoof-glands of other English authors).

*Carpal or knee glands* are the glands commonly represented by a pad of long hair just below the knee or carpus in several Bovidæ.

*Tarsal glands* are the glands represented by a tuft or pad of hair on the inner side of the tarsus of some telemetacarpal Cervidæ (= the calcic tuft or gland of Hodgson, at least in part).

*Metatarsal glands* are the glands represented by a pad or tuft of hair on the outer side of the metatarsus of some Cervidæ and of *Epyceros* amongst the Bovidæ (= the calcic tuft or gland of Hodgson, at least in part).

*Preorbital glands* are the glands in front of the eyes (= sub-orbital and maxillary pits of Owen; sinus lacrymales and glandulæ maxillares of Ogilby; eye-pits of Hodgson; antorbital glands of other English writers).

*Inguinal glands* are the saccular glands of the groin (= inguinal pits of Owen; folliculi inguinales of Ogilby; inguinal glands and pores of Hodgson; groin-glands of other authors).

In addition to these there are glands of less common occurrence, such as the *post-cornual glands* of *Rupicapra*, the *occipital glands* of *Camelus*, the *caudal glands* of *Capra*, the *preputial gland* of *Moschus*, and the *unguicular glands* or glands in the false-hoofs of *Tetraceros*.

## Part II.—ON THE STRUCTURE OF THE GLANDS AND THE SYSTEMATIC RESULTS TO BE DERIVED FROM THEM.

### Family BOVIDÆ.

The subjoined dichotomous analytical key, based mainly on the structure of the feet and upon the specialised cutaneous glands, shows the subfamilies into which the Bovidæ may be provisionally divided on the evidence supplied by these characters. I have preserved all the subfamilies already established by previous authors, and have added a few new ones for the reception of isolated genera which I found could not be included in the divisions to which they had been heretofore assigned without frustrating the attempt to define the groups in question.

The erection of new subfamilies for the accommodation of these aberrant genera appeared to me to be the most expedient course to follow under the circumstances, although some authors may perhaps demur to the separation thus entailed of *Pantholops* from the Antilopinae and of *Oreotragus* from the Neotraginae. Furthermore, I am inclined to think that additional groups of subfamily rank will probably be established in the future. *Boselaphus* and *Tetracerus*, for instance, might perhaps be

wisely and advantageously separated from the African Tragelaphines. Possibly a special subfamily should be erected for *Ammodorcas*, which at present I am unable to classify; and a good case could be made out for splitting up the Rupicaprinæ, which no one can claim to be a homogeneous unit. But our knowledge of the mutual affinities of the various sections of the Bovidæ is so surprisingly incomplete that no attempt at a final classification of them can at present be attempted.

Owing to the impossibility of arranging the subfamilies according to their probable relationships in a linear series, it comes about that in the annexed table divisions of this rank are juxtaposed which have obviously no near relationship to each other. *Oreotragus*, for instance, is probably, as is usually supposed, allied to the Neotraginæ and *Pantholops* to the Saiginæ, Antilopinæ, or Caprinæ. Yet these two genera fall, by the differential characters made use of, under the heading *f'* alongside the *Æpycerinæ*, the *Oryginæ*, and others with which they have certainly, as I at present believe, no close connection. That is one of the obvious defects of such tables as the subjoined, which are commonly much more useful than scientific.

I have made no attempt to include *Oribos* in this key, Lönnberg's recent paper on this form making one conclusion abundantly clear, namely, that the genus must for the present be left by itself in the subfamily Ovibovinæ.

- a. On the front and usually also on the hind leg a large interdigital cleft, forming a gland the orifice of which is a long slit with its upper margin sharply defined by the abrupt descent of the integument between the digits; or else the orifice of the cleft is shorter and the gland more or less tubular, extending up between the bones of the pastern, its posterior wall being formed by a close fold of integument forming the heel-tie inferiorly, so that the orifice of the gland opens downwards between the hoofs.
- b. Preorbital gland nearly half-way between the eye and the nose, not valvular or invaginated, but marked externally by a bare streak of skin studded serially with pores; web of pastern reaching only to the heels, closely folded, the gland tubular with the orifice opening freely into the space between the hoofs ..... CEPHALOPHINÆ (p. 867).
- b'. Preorbital gland occasionally aborted, when present usually a valvular invagination, never marked externally by a streak of integument with serially arranged pores.
- c. Glands equally or approximately equally developed on both front and hind feet.
- d. Muzzle large, naked above as far back as the posterior angle of the nostrils ..... NEOTRAGINÆ\* (p. 879).
- d'. Muzzle small, hairy above almost or quite to the anterior angle of the nostrils.
- e. Pedal glands more or less tubular; the integument of the back of the pastern closely folded at the heels. .... MADOQUINÆ (p. 876).

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\* Based upon observation of *Ourebia* and *Raphicerus*, the other genera being unknown to me.

*e'*. Pedal glands a deep cleft with a long aperture on the front of the pastern, the web extending forwards as a close fold of integument from the heels towards the front of the hoof and separating the cavity of the gland from the space between the hoofs.

ANTILOPINÆ (p. 887).

*e'*. Pedal glands aborted or nearly so on the hind feet.

BUBALINÆ (p. 900).

*a'*. Never a deep interdigital cleft opening by a long orifice, with sharply defined upper margin, on the front of the pastern; pedal glands when present and well developed somewhat flask-shaped with a constricted orifice opening on the front of the pastern above the hoofs (*exc. Rupicapra*), never opening deep in the interdigital cleft above the heels.

*f*. A depression on the lower half of the pastern in front caused by the gradual downward and backward descent of the skin of the middle line towards the heels, where it meets the posterior skin to form the heel-tie, allowing the hoofs to be widely or moderately widely separated apically; only rarely (in *Rupicapra*) does the closely folded integument extend forwards from the heels and shut off the interdigital cleft from the space between the hoofs; pedal gland, when specialised, folded upon itself and opening by a small orifice on the front of the pastern high above the hoofs.

RUPICAPRINÆ \* (p. 848) and CAPRINÆ (p. 859).

*f'*. At most a shallow depression on the front of the pastern: the hoofs joined together almost throughout their basal extent by an interungual band of integument extending forwards from the heels, where it meets at an obtuse or right angle the skin forming the posterior wall of the pastern; it similarly meets that of the anterior wall of the pastern, which forms a continuous surface in the middle line, except where its continuity is sometimes broken for a short distance by the orifice of the pedal gland, which, when present, opens close to the hoofs; thus, except for the glandular infolding, the anterior and posterior walls of the pastern are widely separated from each other in the middle line.

*g*. Hoofs truncated apically, the heels raised high above the ground during progression; (interungual integument hairy throughout; a valvular preorbital gland: muffle large; no pedal glands)..... OREOTRAGINÆ (p. 885).

*g'*. Hoofs pointed, the entire sole and heel in contact with the ground during progression.

*h*. Nasal cavities considerably inflated; skin of the heel-tie posteriorly folded upon itself in correlation with the backward extension of the enlarged heels; (no preorbital or pedal glands; a pair of very large inguinal glands with orifice remote from the mamma)..... PANTHOLOPINÆ (p. 898).

*h'*. Nasal cavities not specially inflated; skin of heel-tie not folded, heels moderate in size.

*i*. A pair of large metatarsal glands on the hind legs; no false hoofs; interungual integument continuously hairy; [no preorbital or pedal glands].

ÆPYCERINÆ (p. 918).

\* This section should, perhaps, be divided into two or more subfamilies, none of the genera being closely related to one another. *Saiga* should possibly come under the heading *f* as the type of a special group *Saiginæ*; but the exact structure of the feet and of their glands is unknown to me.

- i'. No metatarsal glands; false hoofs present; interungual integument naked.
- k. Pedal glands present on all four feet and consisting of a thick-walled, elongated sac gradually lessening in calibre towards the orifice, which is situated close to the summit of the interungual web; or else the gland is small and opens behind a conical excrescence developed from the summit of the interungual web as in *Addax*\* ..... ORYGINE (p. 907).
- k'. Pedal glands absent, except in *Pelea*, where they consist of a thin-walled, compressed, roundish sac with a short and narrow neck, the orifice of which opens some little distance above the summit of the interungual web ..... CERVICAPRINE (p. 911).  
TRAGELAPHINE (p. 921), BOVINE† (p. 932).

### Subfamily RUPICAPRINÆ.

#### Genus RUPICAPRA Blainv.

#### RUPICAPRA RUPICAPRA Linn. (The Chamois.) (Text-fig. 83.)

According to Owen the Chamois has no preorbital glands, but possesses inguinal glands and a gland behind the base of each ear. Mr. Lydekker, on the contrary, states that a small preorbital gland is present‡; and even so recently as 1904 Max Weber ('Die Säugethiere,' p. 675) asserts that the male possesses postauricular glands. The pedal glands were described by Max Tempel.

Living examples of Tyrolean Chamois in the Zoological Gardens show no trace either of the preorbital gland mentioned by Mr. Lydekker or of the post-auditory gland mentioned by Owen and other writers; nor could I detect a trace of them in the only fresh specimens I have been able to examine, namely two newly born kids, or upon dried skins in the British Museum.

The feet of these immature specimens were more like those of Gazelles than of any Antelopes, Sheep, or Goats that I have seen. When the hoofs were pulled apart a triangular interdigital depression was shown. This, however, was both shorter and much shallower than in Gazelles. It became gradually shallower and narrower upwards to its apex, the deepest and broadest part being at its lower end, where it was closed by the interungual web. The skin of this web was folded back in the same way as in Gazelles, but much less deeply, so that the skin forming the back of the glandular depression was separated some distance from that of the back of the pastern. The walls of the depression were somewhat scantily clothed with short hairs. Also, as in Gazelles, the entire interungual web, extending from near the

\* On account of the peculiar structure of the feet this genus should perhaps form the type of a special subfamily, Addacinae.

† These groups are distinguishable by other characters than those supplied by the feet.

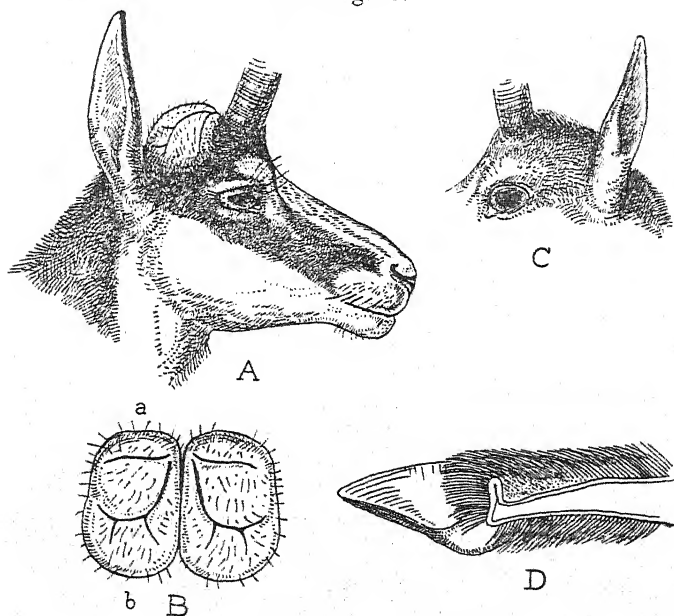
‡ 'Great and Small Game of Europe,' p. 173, 1901. The authority for this statement is not given.

front of the proximal end of the hoof almost to the heels, was clothed with long hairs, the heel-tie itself being naked.

The feet of these immature specimens agreed with those of an adult Chamois described and figured by Max Tempel (*op. cit.* p. 50, pl. xi.), except for the more scanty clothing of hairs on the walls of the depression. In Max Tempel's example the walls of the depression were thickly clothed with long hairs loaded basally with secretion, and the skin forming the posterior wall of the depression was in contact with that of the back of the pastern as in Gazelles.

Judging from the immature examples above mentioned and from dried skins examined in the British Museum, Chamois have four mammae, but no inguinal glands.

Text-fig. 83.



*Rupicapra rupicapra.*

- A. Head of male showing fully developed postcornual glandular swelling.
- B. The glandular swelling from above: *a*, anterior, *b*, posterior end.
- C. Summit of head of adult female drawn on the same day as A, showing absence of swelling.
- D. Foot of newly born kid showing depression on the front of the pastern.

That Chamois possess glands upon the head has been known for many years. These glands have had a curious and confusing history. They have been persistently described as "post-auditory" or "post-auricular," whereas in reality they are immediately

behind the horns and well in advance of the base of the ears. By no possibility can they be described with accuracy as behind the ears. I think Hamilton Smith must have been the first to start this error in 1827. In Griffith's 'Animal Kingdom,' iv. p. 22, he stated that there was a gland behind the ear; but on p. 281 of this volume he described the same gland apparently as occurring behind the horns. In 1836 Owen repeated the statement that they are post-auditory, thus confirming my suspicion that he borrowed many of the facts for his paper from Hamilton Smith. In 1855 the glands were quite correctly figured and described by Von Hessling as behind the horns (*Zeitsch. f. w. Zool.* vi. pp. 265-271, pl. viii.); but in the illustration accompanying this memoir the ears appear to have been added as an afterthought, for they are drawn as projecting from the side of the head-skin much too far forwards, the anterior edge of their bases being in a line with the posterior base of the horns, so that part of the gland, at all events, is behind the ears. The figure, however, is quite wrong in that particular. As is well known, the horns of a Chamois rise vertically nearly over the eyes and the ears are set far behind both. To Owen's mistake and Von Hessling's inaccurate figure must probably be attributed the statement made by Flower and Lydekker ('Mammalia,' p. 12, 1891), by Max Weber (*Die Säug.* p. 675, 1904), and by Lydekker ('Field,' 1909, p. 1100) that the glands in question are post-auditory, the latter even speaking of them as "occipital." Yet, curiously enough, Flower knew at one time that they were behind the horns and in front of the ears, because there is a preparation in the Museum of the College of Surgeons showing their exact position; and in the catalogue there is an entry in his handwriting, giving an accurate description of the preparation with a reference to von Hessling's paper\*. This specimen was received from the Zoological Society in 1877, many years before the repetition of Owen's mistake by Flower in his classical work on the Mammalia.

A further point of interest connected with this specimen is that it was a female. The glands appear as a pair of subcrescentic slits, one behind each horn and about half an inch away from it. This establishes the conclusion that the female possesses the glands as well as the male, although they do not appear to become enlarged at the breeding-season as in the latter. Their appearance in the bucks was recently described by Mr. A. Buxton ('Field,' 1909, p. 1056), who found them in the autumn of the year in various stages of growth, and said that they gave out a strong goaty smell.

In the male Tyrolean Chamois now living in the Gardens the glands began to swell in the latter half of September when the coat began to darken, were at their maximum through November and the first half of December, then gradually dwindled away, and by the end of the first week of January were represented by a flat

\* I am indebted to Mr. R. H. Barne, F.Z.S., for this information.

area of wrinkled skin buried in the hairs of the top of the head. At no time did I see any discharge or secretion coming from them. At their best they projected well above the longest hairs on the parietal area of the head as a pair of rounded cushion-like excrescences of purple skin studded with short hairs and folded into deep intersecting grooves, recalling a pair of cerebral hemispheres marked with a few sulci. Seen from above, the margin is straightish in front up against the horn, lightly convex externally, widely rounded posteriorly, and straight internally, where it is closely in contact throughout its length with that of the opposite side. The surface is convex from before backwards and from side to side; and from the antero-internal angle of each on the upper side two deep sulci descend towards the external border, one close behind the horns, the other backwards and outwards, giving off two backwardly-directed short sulci in its course.

In a male eighteen months old the glandular area showed no signs of swelling as late as November.

In one of the newly born kids I found these postcornual glands represented by a pair of very shallow crescentic grooves entirely concealed in the hairs of the top of the head.

#### Genus OREAMNOS Raf.

OREAMNOS MONTANUS Orl. (The Rocky Mountain Goat.)

(Text-fig. S4, A.)

The presence of glands behind the horns in this species has been recorded by Mr. Hornaday\*, Mr. Frederick Gillett†, and by Mr. Madison Grant‡. Mr. Hornaday described them as "a peculiar bare patch of black oily skin, the size of a half dollar." To this Mr. Gillett added the important information that "under the external skin these glands consist of a soft red tissue saturated with a milky substance, like the udder of a cow. In the specimen at our [London Zoological] Gardens these glands are partially covered up by long hair at the present time [February], but in October and November they are more conspicuous. The older the animal the more pronounced are the glands." According to Mr. Madison Grant the gland, which is as large as half an orange and situated in a half-circle immediately behind each horn, "is sometimes so tough as to wear deeply into the base of the horn." This author cites the presence of this gland as the most striking character of *Oreamnos* as compared with other genera of Rupicaprinae. No doubt his failure to recognise it as the same gland that is found in the Chamois (*Rupicapra*) is to be attributed to the erroneous description of the latter as "post-auricular."

My own notes upon an old male animal living in the Gardens completely bear out what Mr. Gillett said as to the seasonal development of the gland. In this respect it agreed closely with

\* 'American Natural History,' 1904, p. 115.

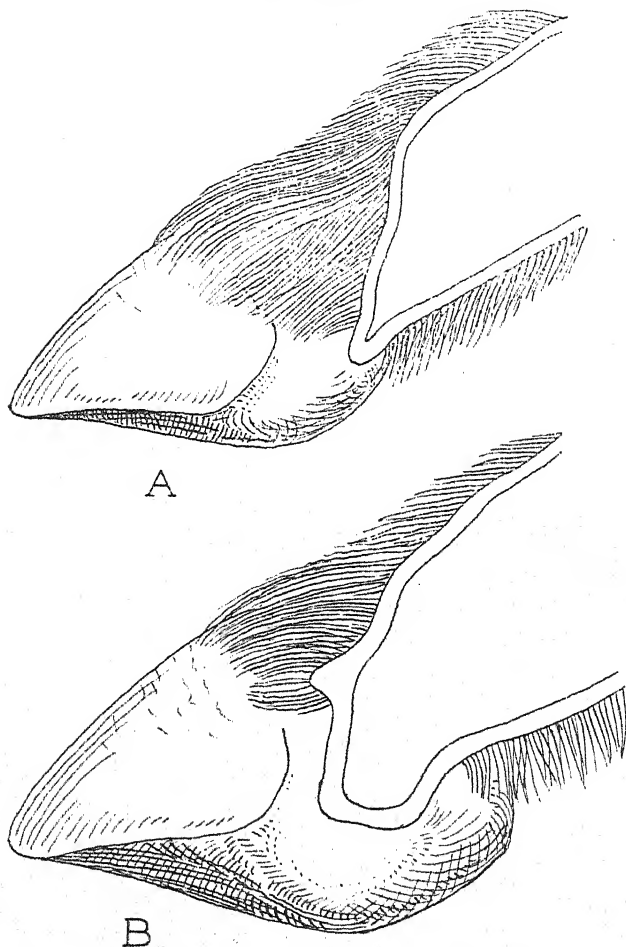
† P. Z. S. 1905, vol. i. p. 56.

‡ Ninth Annual Report of the New York Zool. Soc. p. 12 (reprint).



the homologous gland of the male Chamois; but the integument covering the gland was much more horny and coarser in texture than in the Chamois.

Text-fig. 84.



A. Median vertical section of front foot of *Oreanus montanus*.  
B. The same of *Budorcas tibetanus*.

This Rocky Mountain Goat had no preorbital or inguinal glands. The feet were constructed almost as in Goats (*Capra*); that is to say, there was on the lower part of the pastern in front a deep interdigital depression formed by the abrupt downward and backward slope of the integument to meet that of the posterior

side of the pastern at an acute angle just above the heels, firmly binding the latter together. As in wild and most tame Goats, the walls of this depression were clothed with long hairs. On the hind feet these hairs were clean; but on the fore feet they were stained yellow and stuck together, showing dried scurfy material at their roots and suggesting activity of the sebaceous glands over a considerable part of the area.

The genus *Oreamnos* exhibits puzzling cross-affinities. With the feet and beard of the Goats (*Capra*) are combined the short cannon-bones of the Takin (*Budorcas*), the post-cornual glands of the Chamois (*Rupicapra*), and the short, lightly curved, backwardly inclined horns of *Capricornis* and *Nemorhedus*.

Genus *NEMORHEDUS* H. Sm.

*NEMORHEDUS* GORAL Hardw.

(The Goral.)

According to Hodgson, *N. goral* has no inguinal or preorbital glands, but possesses feet-pits on all four feet. Owen is in agreement with him as regards the absence of the glands in the groin and on the face.

Ogilby also states that the preorbital and inguinal glands are absent, and adds that the pedal glands are large and the mammae four in number.

My own observations agree with these in every respect.

On a flat skin of *N. goral* sent to me from Chamba by Major Rodon, F.Z.S., I found the pedal glands present on all the four feet. They presented a close resemblance both in position and structure to those of Sheep (*Ovis*), opening by a small orifice on the front of the pastern some distance above the hoofs. The orifice led into a slightly dilating hair-lined sac running backwards to the posterior wall of the pastern parallel to the interungual web. Just below the orifice the integument descended obliquely between the hoofs to the heels, where it formed a stout horny tie. This interungual web met the integument of the back of the pastern on the heels almost at right angles. The hair on the back of the pastern extended only for a short distance between the heels; but the interungual integument was covered with long hairs, becoming progressively shorter towards the heel-tie, which was itself smooth and hairless. The hoof itself was short and compressed with the heels high; their web or tie being raised considerably above the ground. Thus not only in the position and structure of the pedal gland\*, but also in the hairiness of the interungual integument and the smoothness of the heel-tie, a very close resemblance could be traced between the feet of *Nemorhedus* and those of *Ovis*.

\* I believe the pedal gland described above was incomplete, since the bones and tissues of the pastern had been to a large extent cut away from behind and there was a small tear in the skin of the bottom of the gland.

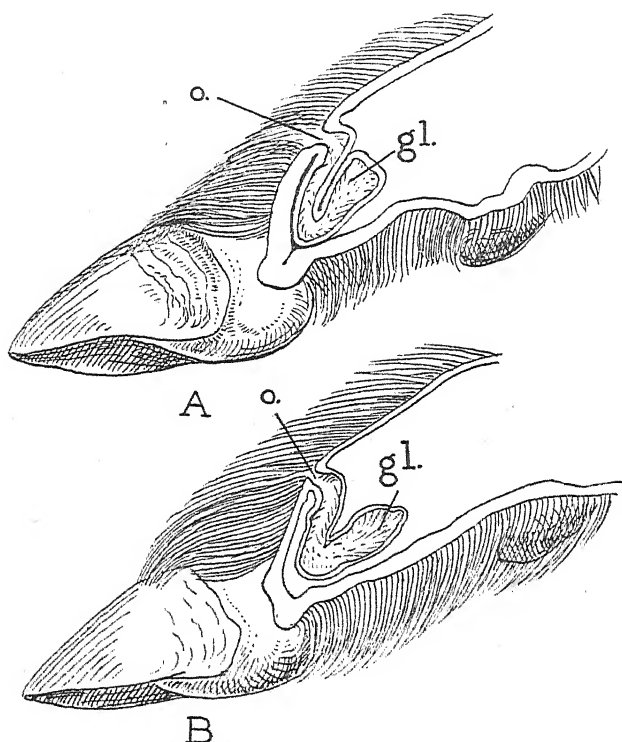
*NEMORHEDUS RADDEANUS* Heude. (Radde's Goral.)

(Text-fig. 85, A.)

The entire skin of an adult example of this species\* from Lao-i-san, near Shensi in Central China, was kindly lent to me by Mr. Edward Gerrard.

The structure of the foot was the same as in *N. goral*, except that the hoofs were rather longer and the pedal gland much

Text-fig. 85.

A. Median vertical section of front foot of *Nemorhedus raddeanus*.B The same of *Capricornis crispus*.

*gl.*, pedal gland; *o.*, its orifice.

(Dry specimens.)

longer and more capacious. Just within the orifice the duct was directed for a very short distance upwards and backwards. It then took a sharp bend downwards and forwards, running close along the interungual web to the heel-tie. At this point it was

\* *Vide* Pocock, P. Z. S. 1908, p. 196.

bent sharply backwards and upwards on itself, the terminal portion which, roughly speaking, ran parallel with the integument of the back of the pastern, being subequal in length to the portion running parallel to the interungual web. The gland was lined with hairs and charged with secretion. Its structure was practically the same on both front and hind feet.

There were two pairs of teats, but no trace of inguinal glands could be detected.

### Genus CAPRICORNIS Ogilby.

#### CAPRICORNIS THAR Hodgs.

(The Nepalese Serow.)

According to Owen this species possesses preorbital glands, but is without inguinal glands. Ogilby, however, asserts that it has inguinal glands and pedal glands and four mammae.

In the example of the Darjiling race (*C. thar jamrachi* Poc.) \*, now living in the Gardens, a distinct but small orifice is observable upon the pastern of the fore foot, and the white hair immediately around it is at times stained yellow, proving that a gland is present and active. This animal is a female nearly five years old; and the preorbital gland is never prominent or turgid as described by Hodgson in the case of the male *C. thar* †. It is represented externally by a circular orifice, from which exude drops of whitish fluid hardening into solid particles, recalling both the appearance and scent of gum arabic. I am unable to state anything about the inguinal glands.

#### CAPRICORNIS (or CAPRICORNULUS) CRISPUS Temm.

(The Japanese Serow.) (Text-fig. 85, B.)

Mr. Edward Gerrard kindly lent me a dried skin of this species.

The preorbital gland consisted of a simple hair-lined pouch with a small subcircular orifice. The pedal glands were well developed on all four feet, and resembled almost exactly in structure those of *Nemorhedus raddeanus*. The feet also were constructed as in that species, though the hairy clothing was longer. There were four teats, but no inguinal glands.

I am also indebted to Mr. E. Gerrard for the opportunity to examine the flat skin of a female of *C. argyrophantes* from Szechuen. On this I could find no pedal glands except a shallow depression on one of the anterior feet, recalling the aborted pedal glands of *Capra*, *Pseudois*, and *Hemitragus*. Moreover, the hair on the front of the pastern did not extend so far downwards between the hoofs as in *C. crispus* and *Nemorhedus raddeanus*. The state of preservation of the feet on this skin does not justify the final

\* Abstr. P. Z. S. no. 55, p. 12, 1908; P. Z. S. 1908, p. 183, fig. 34.

† P. Z. S. 1836, p. 39.]

conclusion that the glands are absent; and until more is known of the pedal glands of the other species referred to *Capricornis*, no certain conclusions can be drawn regarding the taxonomic value of the facts above recorded. If *C. argyrochaetes* prove to be without glands and *C. thar* to have them, there will be a strong *prima facie* case for regarding these species as belonging to two distinct genera. *C. thar* is the type of *Capricornis*, and for *C. argyrochaetes* the name *Nemotragus* Heude will have to be employed.

Finally, it may be added that Owen states that *C. sumatrensis* possesses inguinal glands as well as the preorbital glands—a fact which still further emphasises the importance of the examination of fresh material of this little-known genus.

#### Genus BUDORCAS Hodgs.

##### BUDORCAS TAXICOLOR WHITEL.

(The Bhutan Takin.)

In the living example of this Takin in the Gardens there is no trace of preorbital gland, and none of pedal glands on the fore feet, as may be clearly seen when the animal rears herself up with the hoofs spread against the bars.

##### BUDORCAS TIBETANUS M.-Edw. (The Chinese Takin.)

(Text-fig. 84, B, p. 852.)

Mr. Gerrard kindly allowed me to cut the fore and hind feet of a female example of this species from Szechuen. There was no trace of pedal glands on either the fore or the hind feet. On the fore feet the integument on the anterior surface of the pastern ended in the middle line below in a strong transverse web, beneath which it passed between the hoofs nearly parallel with the proximal edge of the inner surface of the nail, then turned sharply at right angles, forming a strong heel-tie running parallel with the sole of the hoof before turning up to be continued with the skin of the back of the fetlock. As in the Serow (*Capricornis argyrochaetes*) practically the whole of the interungual integument was naked, although anteriorly the hair on the front of the fetlock was continued a little lower, slightly below the transverse web. The hoofs themselves were shaped very much as in *Capricornis*, but the heel-tie was situated more forwards and nearer the proximal edge of the inner lamina of the nail, making the hoofs much less distensible than in that genus.

The structure of the hind foot was essentially the same as that of the front foot, but there was no trace of the anterior integumental web.

There was no trace of inguinal glands, but the four teats on the dried skin were curiously invaginated, giving the appearance of four small symmetrically arranged pits, which I at first mistook for inguinal pouches.

The genera of Rupicaprinae may be distinguished as follows by their cutaneous glands:—

- a. Muffle large, encircling the nostrils below and extending as far as their posterior angle above; a well-developed pedal gland like that of *Ovis* on all four feet.
- b. Preorbital glands present ..... *Capricornis*.
- b'. Preorbital glands absent ..... *Nemorhedus*.
- a. Muffle small; pedal glands, when present, otherwise formed.
- c. A pair of glands behind the horns in both sexes; interdigital cleft deep.
- d. Interdigital glandular cleft opening inferiorly between the hoofs, the heel-tie simple ..... *Oreamnos*.
- d'. Interdigital cleft shut below by a close fold of integument extending forwards from the heels towards the proximal margin of the nail in front ..... *Rupicapra*.
- c'. No glands behind the horns; interdigital cleft shallow ..... *Budorcas*.

### Subfamily OVIBOVINÆ.

#### Genus OVIBOS Blainv.

#### OVIBOS MOSCHATUS Linn. (The Musk-Ox.)

(Text-fig. 86.)

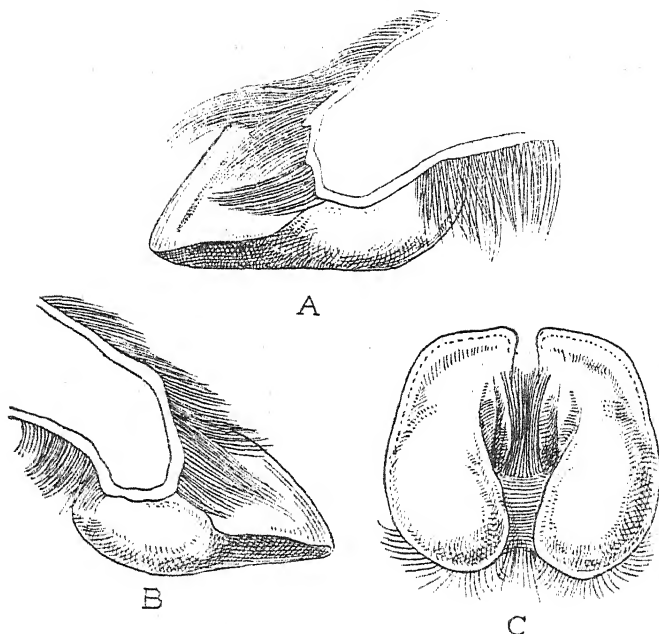
According to Ogilby this animal has four teats, but neither preorbital nor inguinal glands. Of the pedal glands he said nothing. Lönnberg (P. Z. S. 1900, pp. 163-165) agrees as to the number of teats and apparently as to the absence of inguinal glands; but he found in his specimen the preorbital gland well developed, being 23 mm. long, 18 mm. broad, and 8 mm. deep. The interior of the pit was lined with hair, but I cannot judge from the description whether the orifice was valvular as in *Ovis* or simple as in *Capricornis* (the Serow).

Lönnberg also states that he failed to find any pedal glands. I was able to verify this fact on a front and a hind foot of a Musk-Ox which Mr. E. Gerrard kindly allowed me to cut. On the fore foot the skin of the middle line of the pastern in front ends inferiorly in a small web, beneath which the integument runs backwards and downwards to the anterior portion of the heel, then curves upwards and backwards towards the posterior portion of the heel, where it is continuous with the skin of the posterior surface of the pastern. This skin is covered with long hairs, which pass for a short distance between the heels, but the greater part of the integument which ties the heels together is quite naked. Above the heel-tie, however, the interungual integument is covered with long hairs, which largely overlap the proximal inner margin of the nail; and when the hoof is examined from below these hairs appear as a long and thick tuft projecting forwards from the anterior portion of the heel-tie and filling the greater part of the interungual space. Long hairs arising from the bottom of the pastern in front also overlap the proximal anterior portion of the hoof. As is well known, the hoofs are remarkably short

and broad, the antero-external portion of the nail being enormously developed as compared with the small internal portion, the soles and heels being correspondingly large.

The hind foot is very like the fore foot, and has no trace of a gland; nor on the specimen examined did I find any trace of the small antero-superior web, and the integument of the front of the pastern descended more abruptly between the hoofs down to the heels, making a more marked depression between the hoofs than was visible before the front hoof.

Text-fig. 86.

*Oribos moschatus.*

- A. Median vertical section of front foot.
- B. The same of hind foot.
- C. Lower surface of hind hoof.

The systematic position of *Oribos* must for the present be left unsettled. According to Lönnberg, it should rank as a special subfamily, for which the name *Ovibovinae* is retained. Gray \*, it may be added, long ago placed the Takin (*Budorcas*) with *Oribos* in the family *Ovibovidae*; but the evidence that the two are really related is not convincing, and cannot be settled until the anatomy of *Budorcas* is known.

\* Cat. Rum. Mamm. in the British Museum, p. 31, 1872.

## Subfamily CAPRINÆ.

## Genus OVIS L.

(Sheep.)

Ogilby stated that in *O. aries* (Domesticated Sheep) the preorbital glands are large but immovable, the pedal glands small and the inguinal glands absent, adding that there is only a single pair of mammae.

According to Hodgson, *O. ammon*, the Siberian Argali, and *O. ammon hodgsoni* (= *ammonoides*), the Tibetan Argali, have large but immovable preorbital glands, distinct inguinal glands, and pedal glands on all four extremities, whereas *O. musimon*, the Mouflon, for which on that account he created the genus *Caprovis*, differs in having no pedal glands.

Owen ('Anatomy of Vertebrates,' iii, p. 638, 1868) described and figured the pedal gland presumably of a domesticated breed; but according to Isidore Geoffroy the glands are absent in some breeds; most modern text-books and systematic treatises state that the preorbital, pedal, and inguinal glands are present, and that there is a single pair of mammae, a statement with which my own observations are entirely in accord except that there is occasionally an additional pair of small mammae.

I have examined fresh specimens of two wild species, namely, *O. vignei* and *O. musimon*, and a dried skin of *O. canadensis*.

## OVIS VIGNEI Blyth. (The Urial or Gad.)

(Text-figs. 87, 88.)

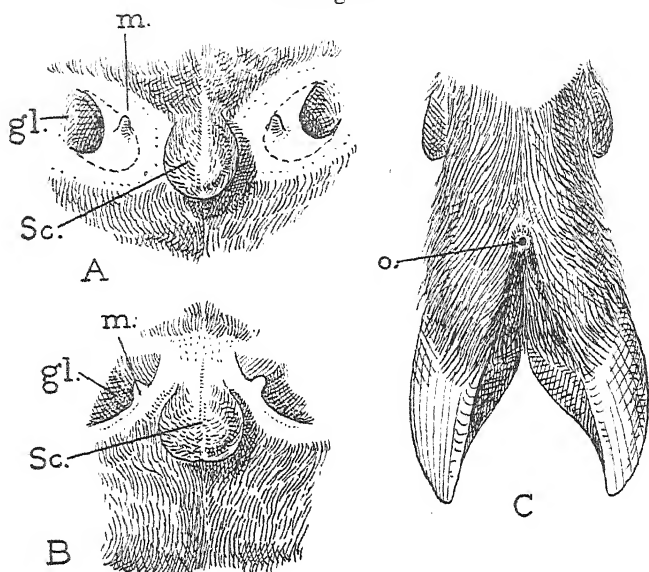
The preorbital gland consists of a hair-lined valvular pocket or invagination closed by a flap of skin forming a movable upper lid. The pocket in captive specimens is commonly blocked with a nearly dry and waxy or quite dry secretion with no definite smell but that of "sheep," and the hairs around the orifice are generally stuck together with the same substance. The dryness of the secretion is probably pathological and due perhaps to insufficiency of green or natural food.

The inguinal glands, two in number, consist of rather shallow pouches, with the deep part underlying the teat, close to which the wide subcrescentic orifice opens. The secretion is yellowish and waxy, and gives off a powerful odour, just like that of the urine of the common House Mouse (*Mus musculus*). The area of skin surrounding the teat and gland is naked. Normally there is a single pair of teats. In one specimen, however, I found an additional smaller pair lying in front of the pair adjacent to the orifice of the gland.

The structure of the feet is very constant. When the hoofs are pulled apart a triangular hairy depression is seen in the middle line of the lower half of the pastern. This depression is caused by the

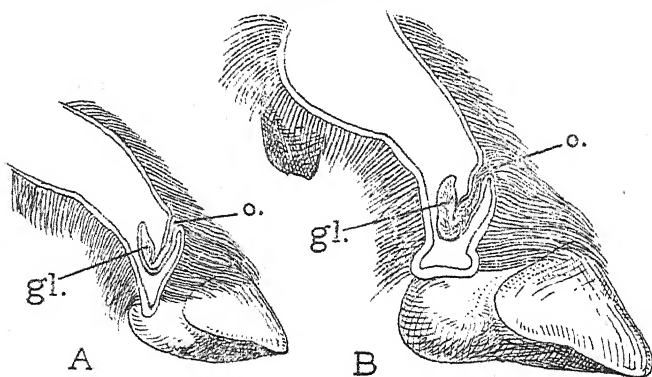


Text-fig. 87.

*Ovis vignei.*

- A. Inguinal region of young male: *m.*, mamma; *gl.*, orifice of gland, the size of the invagination shown by a dotted line; *Sc.*, scrotum.  
 B. The same of lamb three days old, showing the shallow glandular depression (*gl.*).  
 C. Front foot of an adult showing the orifice of the pedal gland (*o.*).

Text-fig. 88.

*Ovis vignei.*

- A. Median vertical section of foot of lamb three days old.  
 B. The same of adult.

*gl.*, pedal gland; *o.*, its orifice.

somewhat abrupt descent of the integument just above the hoofs. It descends straight down to the heels, which are united by a strong tie running for a short distance parallel to the sole of the hoof before turning upwards in continuation with the skin of the back of the pastern. The heel-tie is the only portion of the interungual integument which is hairless, the area above the tie being covered with long hairs which project forwards, overlapping the proximal margin of the nail in front.

The hoofs are short and pointed and the heels of the hoofs well developed, being both high and long, so that the integumental tie between them is raised considerably above the ground.

The pedal gland opens by a small circular orifice near the summit of the triangular depression on the front of the pastern, some distance above the hoofs. The orifice leads into a narrow duct which quickly but gradually expands into the gland. The latter descends along the interungual integument towards the heel, then turns sharply upwards and backwards upon itself for a short distance along the integument of the back of the pastern.

The gland is lined with short hairs, and the secretion is a clear semi-fluid substance with a pleasant scent like toffee (baked butter and sugar), slightly infused with acetic acid.

Of this species I have examined several specimens of various ages from Persia. One example three days old had all the glands developed, the pedal glands being as large relatively as in the adult, the preorbital gland only a little smaller, but the inguinal glands decidedly shallower. I have also noticed that the inguinal pouches are sometimes quite shallow in Sheep of domesticated breeds.

#### OVIS MUSIMON Schr.

(The Sardinian Mouflon.)

This species has the glands of the same structure as in *O. vignei*, with the preorbital gland smaller; but in one specimen I noticed an unexpected difference in the feet, the entire interungual area from a point on a level with the front of the hoof downward including the heel-tie being naked instead of hairy.

#### OVIS CANADENSIS Shaw.

(The Rocky Mountain Bighorn.)

In a dried skin of this species, for which I was indebted to Mr. E. Gerrard, I found the preorbital gland, which Mr. Lydekker has described as minute and almost rudimentary, to consist of a small but very distinct valvular invagination, only differing in its relatively smaller size from that of other species of Sheep. The presence of a pair of inguinal glands was unmistakably indicated and there was a single pair of teats. Remains of the pedal glands showed that these organs open as in ordinary Sheep, and the interdigital area was clothed with hair down to the heel-tie.

*Domesticated Sheep.*

Of Domesticated Sheep I have examined examples of many breeds from different countries without finding any variations of moment in the structure of the pedal, inguinal, or preorbital glands. The rarest specimens were the following:—a lamb of three or four months old from Fair Island between the Orkneys and Shetlands, belonging to Mr. A. J. Sewell; a black lamb of about two months old, probably belonging to a four-horned breed from Caithness in Scotland; an adult short-tailed ram of the breed from the island of Soa in the Hebrides; a Hunia or Fighting Ram from Nepal and a four-horned breed from the same country, both short-tailed; two rams of the long-tailed maned breed belonging to the Hausa tribes of N. Nigeria; and a fat-tailed South-African Sheep belonging to Sir Claud Alexander\*.

In three of these sheep, namely, in the Caithness and Soa specimens and in the Hunia Ram, I noticed that the interungual area was hairy, exactly as in *O. vignei*, and not naked as in the example of *O. musimon* described above.

In no Sheep, domesticated or wild, have I found the pedal glands absent; and in every case where the scent of the secretion was tested it had the sweet odour of toffee. The histology of the pedal glands of *Ovis aries* has been fully described by Max Tempel.

## Genus AMMOTRAGUS Blyth.

## AMMOTRAGUS LERVIA Pall. (= OVIS TRAGELAPHUS).

## (The Barbary Wild Sheep.)

I have had no opportunity of examining a dead specimen of this species; but careful inspection of a living male example gave the following results.

There was no trace of preorbital gland. Inguinal glands also were absent, and there was a single pair of teats. The feet were constructed as in Sheep and Goats; but there was no trace, either upon front or hind feet, of any orifice leading into a special gland such as is present in Sheep. In Sheep the orifice of this gland may be seen at once by superficial scrutiny of the front of the pastern, in spite of the hairy clothing. The most striking peculiarity about the feet of this example of *O. lervia* was the apparent smoothness of the interungual integument and the

\* It is commonly stated in works on Natural History that domesticated breeds of Sheep differ from all the wild species in having long tails. This is not true. Of the above-mentioned Sheep the shortest tail, containing only 5 vertebrae with a short terminal unsegmented portion, was found in the Soa breed. The Fighting or Hunia Ram from Nepal had a tail  $6\frac{1}{4}$  inches long, containing 10 vertebrae. In the Caithness breed the tail scarcely reached the hocks and contained 15 vertebrae. In the Hausa Sheep, on the contrary, the tail nearly reached the fetlocks and was composed of 20 vertebrae, as in a fat-tailed Asiatic Sheep mentioned by Pallas. It may be added that Nepalese Sheep of the Hunia, four-horned, and one-horned races all have short tails, the tail of an adult four-horned specimen measuring only  $3\frac{1}{2}$  inches.

shortness of the hairs clothing the interdigital depression on the front of the pastern.

In the absence of preorbital, of inguinal, and of specialised pedal glands *Ammotragus lervia* agrees with *Pseudois*, *Hemitragus*, and *Capra*, and differs from *Ovis*. The glands, in fact, completely bear out the conclusion suggested by the structure of the skull and certain external features described in text-books, that *Ammotragus* cannot consistently be included in *Ovis* if *Capra* be excluded therefrom.

I do not know who was the authority for the statement found in Mr. Lydekker's work 'Wild Oxen, Sheep, and Goats,' pp. 149 & 226, 1878, that this animal possesses pedal glands. The invariable presence of these glands is cited as characteristic of *Ovis* as contrasted with *Capra*; and the species in question is included under *Ovis*, although subgeneric rank is assigned to it.

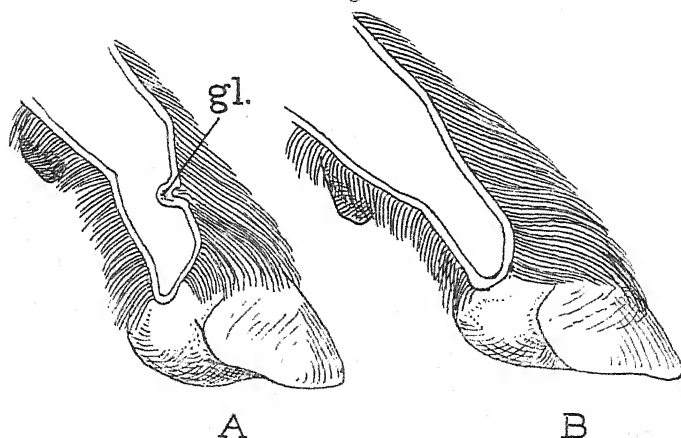
### Genus PSEUDOIS Hodgson.

PSEUDOIS NAYAVUR Hodgson. (The Bharal.)

(Text-fig. 89.)

According to Hodgson, *O. nayaur* has no preorbital glands, but possesses small pedal glands on all four feet and two inguinal glands, marked, however, by vague pores. It was principally on

Text-fig. 89.



*Pseudois nayaur*.

- A. Median vertical section of front foot of female retaining the aborted gland (*gl.*).  
B. The same of the male without trace of the gland.

the absence of the preorbital glands that Hodgson separated this species from *Ovis* as the type of a distinct genus *Pseudois*. Blanford repeats the information supplied by Hodgson, but without quoting him as his authority.

I have examined two fresh examples, male and female, of this species, and can endorse what Hodgson says with regard to the absence of the preorbital gland, though its position was marked by a small patch of naked skin. I found, however, no trace of inguinal glands, and Hodgson himself admits that the pores (invaginations) are "vague." Perhaps the glands he found were mammary glands. As for the pedal glands, I discovered on the fore feet of one specimen (a female) a very small invagination dipping into a subcutaneous glandular patch, exactly like the gland described above as occasionally occurring in Goats. On the hind feet a similar small pocket was present, but there was apparently no differentiated gland. In a full-grown male there was no trace of the gland or the invagination on any of the feet. Except that the interdigital depression is perhaps a little shallower, the feet do not differ structurally from those of Goats. The depression is covered with long hairs, the tips of which overhang the margin of the nail; only the bridge of skin holding the heels together is naked. The practical suppression of all the glands found in typical Sheep is, in my opinion, ample justification for regarding the Bharal as the type of a genus distinct from *Ovis*, quite apart from other structural differences such as those supplied by the skull. Whether or not *Pseudois* can be distinguished from *Capra*, to which it is linked by one of the races of *C. cylindricornis*, is another matter.

Genus CAPRA Linn. (Text-fig. 90, B.)

All authors seem to agree that the preorbital and inguinal glands are invariably absent in this genus; but there is no such unanimity as regards the pedal glands. According to Ogilby they are present; whereas Hodgson says they are either altogether wanting, or present only on the fore feet, and Isidore Geoffroy\* states that they are very rarely present. Hodgson records their occurrence on the fore feet in specimens of three distinct breeds of domesticated Indian Goats, namely the Chyapu, the Sinal, and the Dúgú. He gives, moreover, an illustration of an extracted gland, which shows it to be of the same general structure as in Sheep, although relatively smaller †.

Having examined the feet of many English Goats killed in the Society's Gardens for food, I can endorse the accuracy of Hodgson's statement that the glands are absent in the hind feet and present or absent in the front feet. In the latter, however, they are much more commonly absent than present, and I have never found them so well developed as Hodgson represents ‡. They are, when present, represented by a shallow pocket-like invagination bearing a few short hairs, those that protrude from the orifice being stuck together with secretion. This invagination

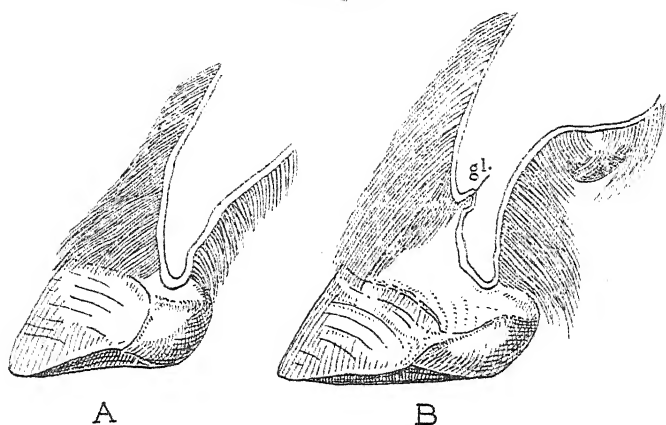
\* Hist. Nat. gén. iii. p. 435.

† J. A. S. Bengal, xvi. pt. ii. pp. 1016-1026, 1847.

‡ Max Tempel also only occasionally found an aborted gland in Domesticated Goats.

occupies the same position as the orifice of the gland in *Ovis*; and this fact, coupled with the close resemblance that Hodgson showed to exist between the glands of *Capra* when well developed and those of the former genus, suggests that the ancestors of existing Goats had glands on the fore feet, and probably also on the hind feet, like those of Sheep. The feet themselves also closely resemble those of Sheep. There is a deep depression between the penultimate phalanges, formed by the abrupt downward slope of the integument of the upper (anterior) side to meet that of the lower side at an acute angle just above the heels, forming a strong sometimes horny union between them. The heels are thus incapable of much distension, whereas the tips and proximal portion of the upper side of the hoofs can be widely separated. The heels are

Text-fig. 90.



A. Median vertical section of front foot of *Hemitragus jemlaicus*.  
B. The same of *Capra hircus* (var. dom.) retaining aborted pedal gland (*gl.*).

high and prominent behind. So far as the hairiness of the interdigital depression is concerned, great variation exists. In some cases it is covered with longish hairs, in others it is quite naked, an intermediate condition existing in others. Seeing how constant a specific character the hairiness of this area is in wild species of Ruminants, I am at a loss to know what explanation to put upon its variability in these domesticated animals, which are supposed to be descended from *C. aegagrus*.

Domesticated Goats have two shallow glandular pouches at the base of the tail beneath, one on each side, close to the anus. I have also found these in *Capra cylindricornis* and *falconeri*.

Of species usually referred to *Capra* I have examined the following specimens, in addition to the domesticated examples alluded

to above, and found no trace of preorbital, inguinal, or pedal glands in any of them :—

*C. agagrus* from Crete : one young male.

*C. sibirica* from Chamba : one young male.

*C. fulconeri* from N.W. India : two adult males.

*C. cylindricornis* from the Caucasus : one young male and one female kid that died at birth.

The structure of the feet resembled that of Domesticated Goats, and the interdigital depression was in all cases hairy, but showed no sign of secretion such as was observable in the example of *Oreamnos montanus* described above.

#### GENUS HEMITRAGUS Hodgs.

HEMITRAGUS JENLAICUS Hodgs. (The Tahr.) .

(Text-fig. 90, A, p. 865.)

According to Hodgson this species has no preorbital, inguinal, or pedal glands. The specimens, three in number, which I have examined bear out this statement, except that in one female example I discovered on the hind feet an abbreviated glandular pocket like that found on the hind feet of a female *Pseudois nayaur*. Sometimes, at least, there are four mammae.

Hodgson included in his genus *Hemitragus*, *H. hylocrius* from the Nilgiri Hills; but I cannot find any evidence that he examined a specimen of that species for the points mentioned in his generic diagnosis. He separated *Hemitragus* from *Capra* because of the larger size of the "muffle" or naked skin at the end of the nose, the alleged presence of four teats, and the absence of pedal glands, which he himself admits may be altogether absent in *Capra*. According to Blanford, however, *H. hylocrius* has but a single pair of teats, thus agreeing with typical Goats.

Hodgson states that the male Tahr has a strong Caprine odour. It is true that in the winter and early spring the animal smells strongly; but the odour is exactly like that of a Cormorant or Frigate-Bird, and not like the odour of *Capra agagrus* or *fulconeri*.

Judged by their glands, the genera of Caprinae fall into two categories, as follows :—

- a. With well-developed preorbital, pedal, and inguinal glands, the latter not always invaginated in domesticated breeds..... *Ovis*.
- a'. Without preorbital and inguinal glands; pedal glands, when present, represented by a very shallow depression, except in some Indian Domesticated Goats, where glands resembling those of *Ovis* are found on the fore feet.

*Ammotragus*, *Pseudois*, *Hemitragus*, *Capra*.

## Subfamily CEPHALOPHINÆ.

## (The Duikers.)

According to Owen the following species of this subfamily have inguinal pits and preorbital glands lodged in a depression of the maxilla:—*Cephalophus silvicultor*, *grimmii* (= *mergens*, *burcheilli*, *grimmii*), *monticola* (*perpusilla*, *pygmaeus*), *maxwelli*.

Two species were examined by Ogilby, namely, *C. monticola*, cited as *Tragulus pygmaeus*, and *C. grimmii*, cited as *Sylvicapra mergens*. According to this author *C. monticola* has neither inguinal nor interdigital glands, whereas in *C. grimmii* there are small interdigital glands and distinct inguinal glands, both species having oblong maxillary [preorbital] glands lodged in depressions of the maxilla. Ogilby also records the presence of two pairs of mammae in this genus\*.

The preorbital gland is described in most recent systematic works as consisting externally of a bare streak of skin studded with a series of pores and situated some distance in front of the eye of the corresponding side. Weber† describes in detail the histological structure of the gland and the nature of its secretion in *C. pygmaeus* [= *monticola*], points out the difference it presents in the male and the female, and gives a list of the species in which he had observed its external form, together with much other interesting matter. The pedal glands do not appear to have been described.

## Genus GUEVEI Gray ‡.

## GUEVEI MAXWELLI H. Sm. (Maxwell's Duiker.)

## (Text-figs. 91, A, &amp; 92.)

In a female example from Portuguese Guinea, presented by Dr. Ansorge, the external streak of the preorbital gland was markedly bent downwards at its posterior end towards the anterior corner of the eye, its lower margin being therefore concave. It was studded with about 25 vertically elongate pores, forming a single series, from each of which a few short hairs arose. With pressure, liquid drops of secretion could be easily squeezed from the pores. The gland itself underlying the bare streak did not

\* The specific names *perpusillus* and *pygmaeus* have been assigned to the so-called Royal Antelope, *Neotragus pygmaeus*; and Sclater and Thomas cite *Tragulus pygmaeus* of Ogilby in the synonymy of *Neotragus pygmaeus*. This view is, I think, incorrect, because Ogilby described the preorbital glands of *Tragulus pygmaeus* and of *Sylvicapra mergens* in exactly the same terms as "glandulae maxillares oblongae"; and since *Sylvicapra mergens* is admittedly a Cephalophine, one must infer that Ogilby's *Tragulus pygmaeus* also belonged to that subfamily and not to the Neotraginae. That Owen's *Antelope perpusilla* and *pygmaeus* were also Cephalophines is clearly indicated by his placing them with other species of *Cephalophus* in a group characterized by "maxillary" as opposed to "suborbital pits." Moreover, he quotes S. Africa as the locality of *perpusilla*, whereas *Neotragus pygmaeus* comes from Liberia.

† Arch. mikr. Anat. xxxi. pp. 507-539, 1888.

‡ Reasons for the adoption of this genus are given below (pp. 874-876).

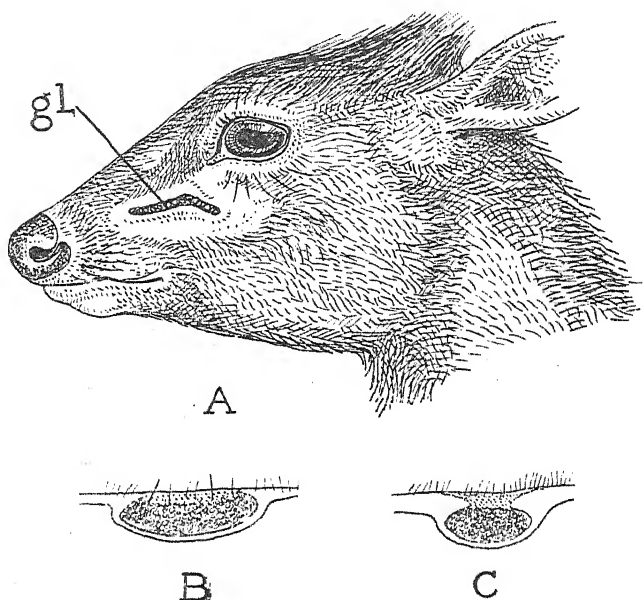


differ in structure and consistency from that of *G. melanorheus* and *Sylvicapra coronata* described below. When alive the animal had the habit, not noticed in other Duikers, of rubbing the glandular area against one's hand when presented to her.

There were no inguinal glands, but two pairs of teats were present.

The pedal glands were well developed. The skin of the back of the pastern extended right down to the heels, forming a strong union between them. It was then folded sharply back upon itself, as far as the false hoofs, to form the posterior wall of the gland. At its deepest or upper part the gland formed a laterally

Text-fig. 91.

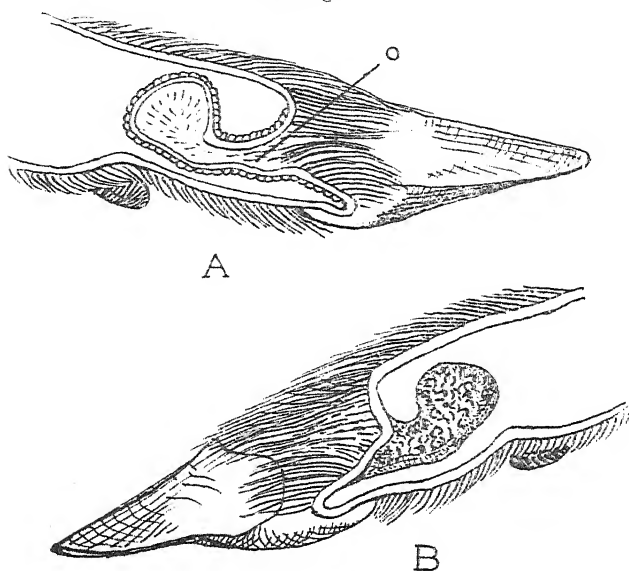


A. Head of female of *Guereza marwelli*, showing the preorbital gland (gl).  
 B. Longitudinal section of the preorbital gland of *Sylvicapra coronata*.  
 C. Transverse section of the same.

compressed subcircular sac which communicated with the triangular interdigital depression, seen when the hoofs were pulled apart, by means of a narrow tube with a gradually expanding subcircular orifice. This interdigital depression was formed by the folding back of the skin of the anterior side of the pastern some distance above the proximal margin of the hoof, the infolded portion forming the anterior wall of the gland and constituting a somewhat deep anterior interdigital web which did not project nearly so far inferiorly as the posterior shallower but stronger

web tying the heels together. The walls of the interdigital depression were thickly covered with long hairs projecting downwards over the proximal margin of the nail, those on the anterior side of the posterior web being especially long, so as to conduct the secretion downwards between the heels of the hoofs. The dilated cavity of the glands was beset with short scattered hairs which gradually lengthened towards the orifice of the gland. The secretion itself was white and sticky, with a repulsive odour of dog's faeces mixed with acetic acid.

Text-fig. 92.

*Guevei maxwelli*.

- A. Median vertical section of hind foot: o., orifice of pedal gland.  
B. Front foot dissected to show the gland entire.

(Fresh specimens.)

In another female specimen from Sekondi also referred to *G. maxwelli*, the preorbital streak, although lightly concave downwards, was not so abruptly angled at its posterior end as in the one described above. The streak was 18 mm. long, 2 mm. wide, and had a row of about 20 vertically elongated pores, from each of which a few small bristles arose. Drops of fluid could be squeezed in the same way from these orifices. There were no inguinal glands, and the pedal glands resembled those of the first-described specimen.

The absence of the inguinal glands in these two specimens of *G. maxwelli* suggests that Owen was probably wrong in assigning these organs to the species, for it does not seem probable that

such a character is subject to individual variation within specific limits. I suspect, moreover, that Ogilby was correct, and, by implication, that Owen was in error, in stating that inguinal glands are absent in *G. monticola*, since the latter seems to be nearly allied to *G. macwelli*. But I cannot doubt that Ogilby was wrong in saying that pedal glands are absent in *G. monticola*.

*GUEVEL AEUATORIALIS* Matsch. (Text-fig. 93, A, B.)

The cut foot of a dried skin given to me by Dr. Christy, who shot the animal in the Chagwe forest, Uganda, had a gland of nearly the same structure as in *G. melanorheus*. The foot of this specimen differs in colour from that of *G. macwelli*, being brown all over and showing no white patch just below the false hoofs on the back of the pastern and no white on its front close to the triangular interdigital depression.

The similarity in the structure of their pedal glands favours the view that *G. melanorheus* and *G. aequatorialis* may be sub-specifically and not specifically distinct.

*GUEVEL MELANORHEUS* Gray. (Text-fig. 93, C.)

A single young specimen from Angola presented by Mr. H. F. Varian.

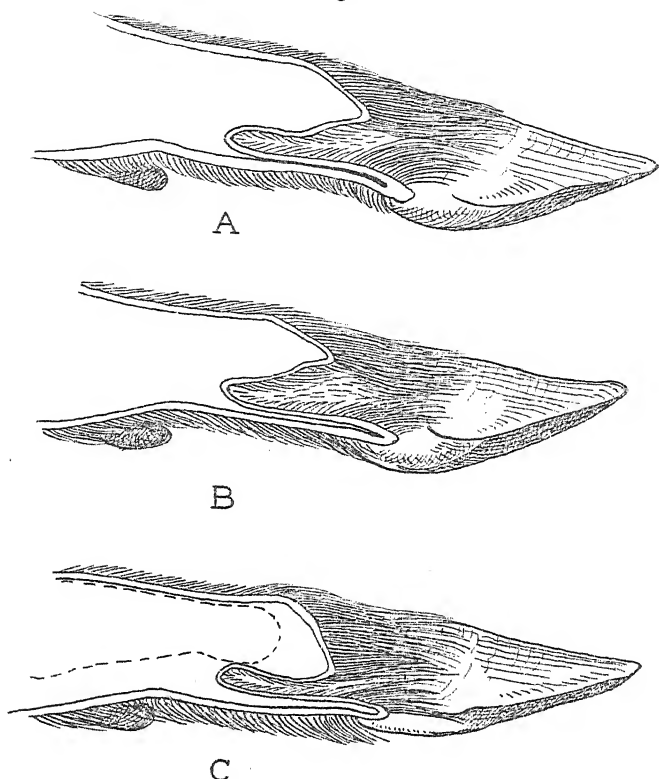
As in *G. macwelli*, the preorbital streak was lightly concave below, but its curvature was less abrupt and situated farther forwards than in Dr. Ansorge's example from Portuguese Guinea. The streak was 22 mm. long and 1 mm. wide, studded with a single series of circular pores, from each of which a single short hair arose. The gland itself, when extracted, measured about 27 mm. long, 10 mm. wide, and 5 mm. in vertical depth. In section, both longitudinal and transverse, it was pale externally, with its central third forming a dark core. Under slight pressure drops of clear fluid, like liquid gum tragacanth, could be squeezed from the pores. When rubbed between the fingers it became, as it dried, quite sticky, giving out a faintly aromatic odour like that of black-currant tea. Under hard pressure pale whitish-grey maggot-like threads could be expressed from the pores.

Inguinal glands were absent as in *G. macwelli*.

The feet were constructed as in the last-named species, with the marked difference that the pedal gland consisted of a simple narrow cylindrical tube not extending so far as the false hoofs and showing no sign of expanding between the bones into an enlarged laterally compressed dilatation.

Although superficially *G. macwelli* and *G. melanorheus* are so much alike that it has been suggested that they be regarded merely as subspecies, it appears to me that the difference in the structure of their pedal glands entitles the two to specific separation, at all events until further examination has shown that this character has not the value here claimed for it.

Text-fig. 93.



A. Median vertical section of hind foot of *Gnuevi æqua*

B. Do. of front foot of the same.

C. Do. of hind foot of *G. melanorheus*.

(All dried specimens.)

#### Genus CEPHALOPHUS H. Sm.

##### CEPHALOPHUS DORSALIS Gray. (The Bay Duiker.)

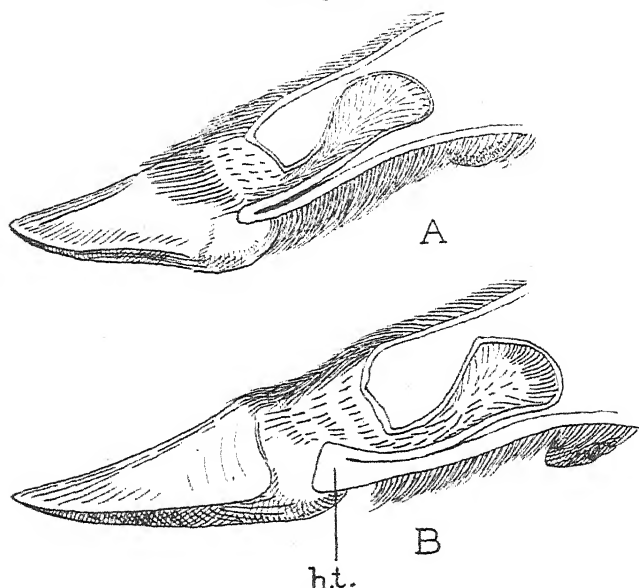
A single example from Sekondi presented by Capt. C. H. Armitage.

The preorbital streak was straight, 22 mm. long, 1 mm. wide, and studded with a single row of 14 pores, from which grey-coloured fluid could be pressed.

Inguinal glands were well developed and widely separated by a space of 42 mm. from the two mammæ of each side. There was only a single pair of these glands. Each consisted of a long sac very gradually expanding internally from the orifice, the walls of

the bottom third of the pocket being corrugated and ridged. The secretion was yellow and sticky. The structure of the feet was almost the same as in the species already described, except that the fold of integument forming the web at the heels was enormously thickened and horny, forming a very strong union between the two hoofs behind. Moreover, this interdigital depression was only scantily clothed with shortish hairs, the tips of which scarcely overlapped the margin of the nail of the hoofs, except

Text-fig. 94.



A. Median vertical section of foot (? front or hind) of *Sylicapra grimmii*, subsp.?  
 B. The same of hind foot of *Cephalophus nigrifrons*. h.t., heel-tie.

(Both dried specimens.)

quite in front. The pedal gland itself was not dissected out, but its circular orifice was apparent. Apart from other features, *C. dorsalis* differs from the species of the *macrilelli* group in possessing inguinal glands; and in this connection it may be noted that Owen records the presence of inguinal glands in *C. silvicultrix*, one of the larger species of the genus usually considered to be related to *C. dorsalis*.

**CEPHALOPHUS NIGRIFRONS** Gray. (The Black-fronted Duiker.)  
 (Text-fig. 94, B.)

A female example of this species, kindly lent to me by Mr. Gerrard, agreed with *C. dorsalis* in possessing a pair

of inguinal glands consisting of deep subcylindrical pouches, with the orifices remote from the mammae. The interdigital cleft was scantily hairy and the heel-tie was very thick as in *C. dorsalis*; and the pedal gland on all four feet consisted of a long expanded sac with a small orifice, as in *G. macralli* and in *S. coronatus*.

CEPHALOPHUS SILVICULTRIX.

(The Yellow-backed Duiker.)

In two dried and flat skins from the Cameroons, kindly given to me by Rowland Ward, Ltd., I found the feet and pedal glands constructed as in *C. nigrifrons*. About the inguinal glands on these skins I can affirm nothing. Owen, however, says they were present in the species.

Genus SYLVICAPRA Ogilby.

SYLVICAPRA CORONATA Gray, 1842.

subsp. CAMPBELLIE Gray (?) 1843\*.

Of specimens referred to this species, I have examined several from various parts of Nigeria, including two young males from Sokoto, presented by Major Searight, and one from Ibadan in the Yoruba country, presented by Mr. T. Christ.

In all of them the preorbital streak was lightly concave upwards, thus differing in shape from that of the Duikers of the *macralli* group, and also, though in a lesser degree, from that of *C. dorsalis*. The streak was studded with a series of 15 or more pores, from which fluid secretion with a pleasant aromatic odour could be squeezed. Under continued pressure black coiling worm-like threads of a waxy consistency exuded.

A pair of inguinal glands consisting of wide but (in the young) shallow pits were present. They were much shallower than in *C. dorsalis*; but their orifices, as in that species, were situated a long way from the two mammae on each side, lying in fact just on the femoral side of the fold or crease between the inner surface of the thigh and the abdomen; and, as in *C. dorsalis*, the whole inguinal and mammary area of the abdomen was naked as far out as the glandular orifices. The secretion of the inguinal glands smelt like sour milk in two examples, but had an objectionable faecal odour in another.

The feet were constructed as in other species of this group,

\* According to Gray (Cat. Rum. B. M. p. 23, 1872), *C. campbellie* was in 1872 represented in the British Museum by a single skin from West Africa, which he marked interrogatively as having been obtained at Sierra Leone. The skin agrees tolerably closely with the Nigerian examples that I have seen. I think, therefore, that Gray was probably correct in assigning his type to West Africa; and that it was an error to suppose that the name *campbellie* belongs to a Natal form of *Sylvicapra* (Lydekker, 'Game Animals of Africa,' p. 142, 1908). *S. coronata* Gray, from Senegambia, appears to me to be a paler form of the same species.

but the walls of the triangular interdigital depression leading to the gland were very sparsely clothed with quite short hairs, much fewer and shorter than in *C. dorsalis*. Only at the inferior margin of the side walls of the depression were there long hairs overlapping the proximal edge of the nail of the hoof. The gland itself consisted of a large laterally compressed sac, very much like that of *G. maxwelli*, but with the narrowed portion much shorter and wider, and with no long hairs jutting from the orifice, the walls of the sac being clothed with very short sparsely set hairs, like those of the triangular depression. As in *G. maxwelli*, the glandular tissue could be traced not only over the walls of the gland itself but from the commencement of the anterior web of the hoofs to that of the posterior web. There was, however, no secretion in the glands.

My observations on this species agree with those made on *S. grimmii* by Ogilby, who stated that both inguinal glands and pedal glands were present, the latter being small. Owen also found inguinal glands in *S. grimmii*.

In an odd foot of a *Sylvicapra* closely related to the typical *S. grimmii*, and given to me by Mr. Gerrard (text-fig. 94, A) I found pedal glands resembling in all essential points those of the legs of the examples identified above as *S. coronata*.

The features to be noticed in connection with the cutaneous glands of the Cephalophinae are the general constancy of the structure of the preorbital gland and of the feet and the minor differences presented by each. The preorbital gland is always large, oval, tough and india-rubbery in consistency, is situated farther forwards than in other Antelopes, and has no valvular invagination of the skin connected with it as in Gazelles, Sheep, Dik-Diks, and others. Instead of this it communicates with the exterior by means of a series of setiferous pores placed on a narrow strip of bare integument. It differs, in fact, from that of all other Ruminants.

The structure of the feet, too, is very uniform. They do not, however, differ materially from those of *Madoqua*, as illustrated by *M. phillipsii*, nor from genera of Neotraginae that I have examined, namely *Ourebia* and *Raphicerus*. Only in one little point is there, within my experience, a constant difference. Whereas in the Madoquinae and Neotraginae the web joining the heels is covered continuously with long hairs, in the Cephalophinae the back of this area of integument is always naked for a longer or shorter distance.

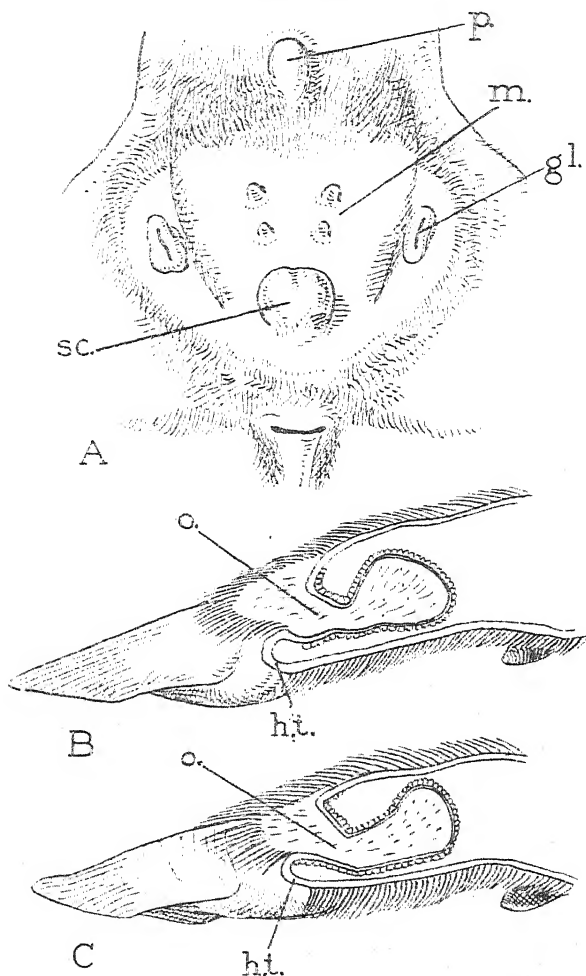
Another peculiar feature of the Cephalophinae is the wide separation of the inguinal glands, when present, from the mammae. In this particular, however, they resemble some Tragelaphinae and *Pantholops*.

In my opinion the absence of the inguinal glands\* in the forms

\* This difference, as well as others, between *melanorheus* and *dorsalis* was noted on the same material by Mr. F. E. Beddard (P. Z. S. 1909, i. p. 181).

above identified as *macruxelli*, *aequatorialis*, and *melanorheus*, points to their generic separation from those referred to *dorsalis*,

Text-fig. 95.



*Sylvicapra coronata.*

- A. Inguinal region of male: *p.*, penis; *m.*, mammae; *gl.*, orifice of gland;  
*sc.*, scrotum.  
 B. Median vertical section of front foot.  
 C. The same of hind foot.

*o.*, orifice of gland; *ht.*, heel-tie.

(All fresh specimens.)



*nigritrons*, and *coronata*, of which *abyssinica*\* is, I think, a subspecies.

It is, moreover, well known that the group exemplified by *coronata* differs from that exemplified by *dorsalis* in the markedly more upright inclination of the horns. If generic importance be attached to that character, a proceeding desirable on the grounds of the unwieldiness of the genus *Cephalophus* as at present recognised, the genus can be split at all events into three genera which may be distinguished as follows:—

- |  |                      |
|--|----------------------|
| a. Inguinal glands absent .....  | <i>Guerci</i> .      |
| a'. Inguinal glands present, consisting of a pair of deep pouches, the orifices of which are remote from the mammae. |                      |
| b. Horns inclined backwards in the plane of the face; ears short .....   | <i>Cephalophus</i> . |
| b'. Horns inclined upwards and backwards, forming an obtuse angle with the plane of the face; ears long .....        | <i>Sylvicapra</i> .  |

The type of the genus *Guerci*, as selected by Messrs. Schater and Thomas, is *maecelli*, with which *equatorialis* and *melanorheus* must be associated. The type of *Cephalophus* is said to be *silvicultrix*, a species in which Owen affirms the existence of inguinal glands. As defined above, the genus also contains *dorsalis* and *nigritrons*. The type of *Sylvicapra* is *mergens*, but *grimmii* appears to be the oldest name given to the species.

For the characters of *Tetraceros*, usually referred to the *Cephalopinae*, see p. 921.

#### Subfamily MADOQUINÆ.

##### Genus MADOQUA Ogilby.

(Dik-diks.)

The available evidence suggests that the species of this genus possess preorbital and pedal glands, but are without inguinal glands. In the case of *M. saltiana*, both Owen and Ogilby are in agreement about the presence of preorbital and the absence of inguinal glands, and Ogilby adds that the pedal glands are also present.

MADOQUA PHILLIPSII Thomas. (Lort Phillips's Dik-dik.)

(Text-fig. 96.)

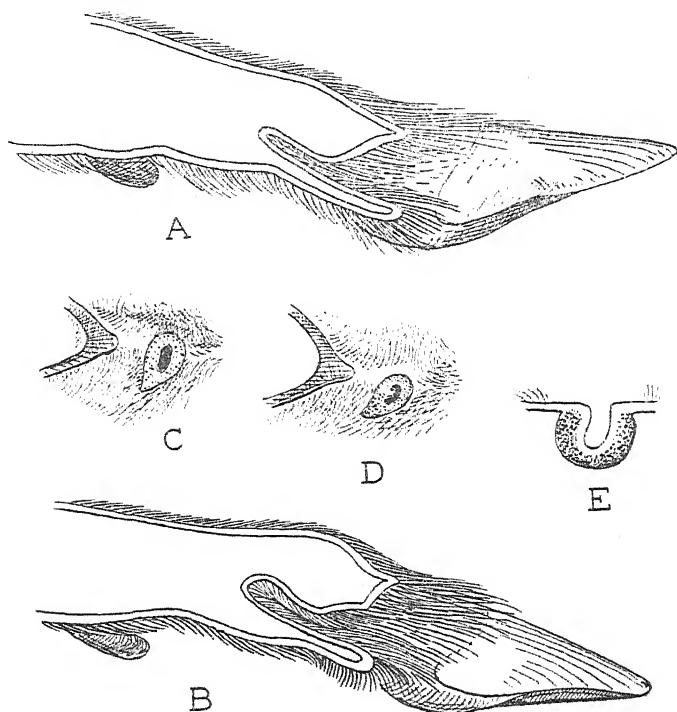
Of this species I have examined, in the fresh state, one example which agreed with the specimens of *M. saltiana* seen by Owen and Ogilby in having preorbital and pedal glands, but no inguinal glands. Mr. Beddard also noted the absence of inguinal glands (P. Z. S. 1909, i. p. 188).

The preorbital glands were small. The orifice was a small vertical crescentic slit, with its concavity looking backwards,

\* I here adopt, without prejudice, Mr. R. C. Wroughton's opinion that *S. abyssinica* differs from the southern form *C. grimmii* in the shortness of its ears. It is quite immaterial to the work in hand whether *abyssinica* be specifically or subspecifically distinct from *grimmii*, since the close relationship between the two is admitted by everyone.

situated in the middle of a naked oval patch of skin just in front of the orbit. The orifice led into a shallow integumental pocket, dipping into the substance of the black underlying gland. Under pressure thickish black secretion could be squeezed from the orifice.

Text-fig. 96.

*Madoqua phillipsii.*

- A. Median vertical section of front foot.
- B. The same of hind foot.
- C. Preorbital gland with orifice distended.
- D. Ditto ditto closed.
- E. Ditto in section.

The two halves of the feet were united in the middle line by two "webs," an anterior and a posterior, the posterior extending as far downwards as the heels and constituting the posterior wall of the interdigital space, the anterior being some little distance above the proximal margin of the hoofs, which were thus capable of much greater distension anteriorly than posteriorly. Beneath the anterior web, the integument receded obliquely backwards and upwards, and gradually passed into the anterior wall of a short subcylindrical tube running upwards

between the phalanges, the posterior wall of this tube being formed by the posterior web of integument. In longitudinal section the gland had the appearance of a narrow cylindrical tube opening by a wide orifice into the interdigital space. The tube and this space were alike lined with hair, which on the lower lip of the orifice formed a longish tuft to guide the secretion down between the heels of the hoofs. The posterior web was continuously hairy all along its back and inferior edge.

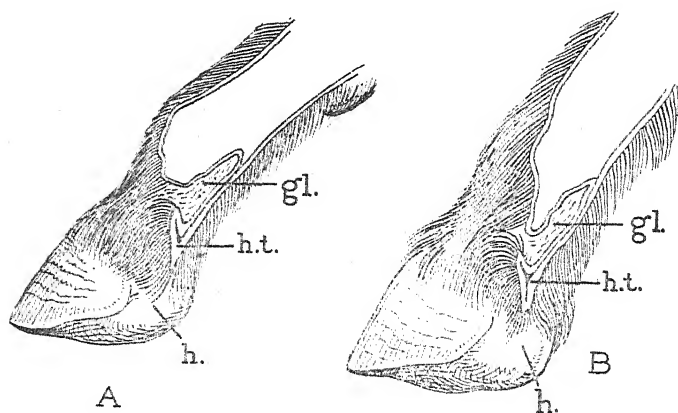
### Genus DORCOTRAGUS Noack.

DORCOTRAGUS MEGALOTIS Menges. (The Beira.)

(Text-fig. 97.)

Of this rare and anomalous Antelope I have seen only the dried skins in the British Museum. Through the kindness of Mr. Oldfield Thomas I was enabled to examine the pedal glands of one of these; and their structure convinces me that *Dorcotragus* is allied to *Madoqua*, but adapted to a mountainous

Text-fig. 97.



*Dorcotragus megalotis.*

A. Median vertical section of hind foot.

B. The same of front foot on a slightly larger scale.

gl., gland; h.t., heel-tie; h., heel.

(Dried specimens.)

habitat. The feet have acquired a superficial resemblance to those of Goats and Sheep, owing to the shortness of the nail and the great development of the sole and heel of the hoofs, the latter forming large cushion-like pads. The strong integumental bridge joins the hoofs together just above the heels; and the anterior edge of this is raised so as to form an upstanding lower lip to the orifice of the gland. The latter is a depressed elongated

pouch, recalling that of *Madoqua phillipsii*, except that the orifice is much smaller in consequence of the ridge-like lower rim. This rim seems to be developed in connection with the vertical position of the feet when the animal stands, not only increasing the size and strength of the interdigital union, but serving to check the otherwise uninterrupted downward flow of the secretion from the gland by forming a barrier, above which it accumulates. The pocket of the gland is somewhat sparsely lined with short hairs; those on the upstanding lower rim of its orifice are longer, serving to conduct the secretion outwards, as in *Madoqua*. It is noticeable that in *Raphicerus campestris* and *Madoqua phillipsii* the entire interdigital integument is covered with hair, there being no naked space behind the heel-tie such as is seen in the species of Cephalophinae examined by me. The deep depression between the penultimate phalanges of the foot into which the gland opens resembles that of Sheep and Goats.

On the dry skin I can find no trace either of preorbital or inguinal glands, and there appears to be a single pair of teats.

Messrs. Sclater and Thomas, though apparently not without misgivings ('Book of Antelopes,' iii. pp. 1, 2, 1897), placed this Antelope in the subfamily Antilopinae, "near the Gazelles," and considered as "superficial" the "resemblance it bears to certain members of the subfamily Neotraginae." It appears to me, however, that its affinities, as attested by the horns, skull, muzzle, and coloration, not to mention the apparent absence of inguinal glands and the structure of the pedal glands, are more *Madoquine* than *Gazelline*.

Using the feet and preorbital gland as a basis, these two genera may be distinguished as follows:—

- |  |                      |
|--|----------------------|
| a. Hoofs more or less elongate, with normal sole and heels; heel-tie formed by a simple fold of integument; a preorbital gland present.....  | <i>Madoqua</i> .     |
| a'. Hoofs short, with pad-like soles and heels; heel-tie forming a double fold, the anterior fold projecting as a ridge constituting a kind of lower lip to the orifice of the pedal gland; no pre-orbital gland ..... | <i>Dorcotragus</i> . |

#### Subfamily NEOTRAGINÆ.

#### Genus RAPHICERUS H. Sm.

RAPHICERUS CAMPESTRIS Thunb. (= *Pediotragus tragulus*).

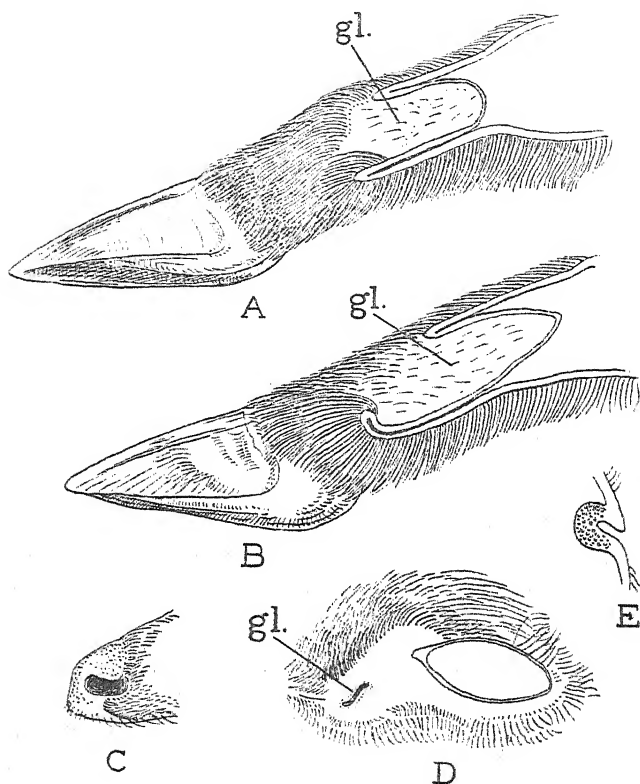
(The Steinbok.) (Text-fig. 98.)

The presence of preorbital and inguinal glands was recorded by Owen; and according to Max Weber, who cites the species under the names *Pediotragus tragulus* and *rufescens*, the preorbital glands are present in both sexes.

Of this species I have examined two old stuffed examples, which the Committee of the Bristol Museum and Art Gallery kindly permitted Mr. Herbert Bolton, F.R.S.E., F.Z.S., the Curator, to send to me.

Neither specimen showed any trace of inguinal glands. This, however, cannot be regarded as satisfactory evidence of their absence, since the skins were mounted and dried.

Text-fig. 98.



*Raphicercus campestris.*

- A. Median vertical section of hind foot: *gl.*, pedal gland.
- B. The same of front foot.
- C. Muffle or rhinarium.
- D. Ocular region of female showing orifice of preorbital gland.
- E. Section of the same gland.

The preorbital glands were placed near the anterior edge of a large area of naked skin in front of the eye. The orifice formed a small oblique slit, with a slight sigmoid curvature. This led into a scantily hairy pocket, dipping into the gland, which, as in *Madoqua phillipsii*, formed a small, nearly black mass. The upper margin of the orifice formed a kind of lid over the pocket. The gland was larger in the male than in the female.

The pedal glands were well developed, but different from those of *Madoqua*. On both front and hind legs they consisted of large wide-mouthed deep pouches passing up between the antepenultimate phalanges of the feet, and opening some distance above the proximal margin of the hoofs. The anterior wall of each was formed by a closely folded web, and the posterior by an equally closely folded posterior web; but neither of these webs extended so far down the foot as in *Madoqua*, the posterior web of the hind foot not nearly reaching the heels, and extending only a little farther than in the *Tragulina*, and reaching only a little farther than the anterior web. This suggests that the heels, as well as the rest of the hoofs, are capable of very wide separation. On the front foot, on the contrary, the posterior web was longer, and reached almost to the heels, extending considerably lower than the anterior web. Its inferior extremity, moreover, was turned slightly forwards for a short distance, making a distinct ridge, something like that of *Dorcotragus*. Although the walls of the pocket were only scantily clothed with hair, the rest of the interdigital space was clothed with long hairs, and the edge of the posterior web forming the posterior lip of the pocket was furnished with long hairs projecting downwards, as in *Madoqua* and *Dorcotragus*. There were two pairs of teats.

RAPHICERUS sp.? or NESOTRAGUS sp.?

I am indebted to Mr. Gerrard for a front and a hind foot without supplementary hoofs, and therefore referable probably either to *Raphicerus* or *Nesotragus*. These are worth describing, because they are structurally nearly intermediate between the feet of *Raphicerus campestris* and of *Ourebia nigricaudata*.

In the hind foot the interdigital cleft was open in front throughout nearly the whole of its length, being only slightly overlapped above by a short angular fold of integument. Its posterior wall descended with a gradual curvature downwards, meeting the skin of the back of the pastern considerably nearer the heels than in *R. campestris*, and forming a strong thickened tie, which was turned slightly forwards.

The interdigital cleft on the front foot hardly differed from that of *Ourebia nigricaudata*, except that its upper extremity was overlapped to a greater extent, although not so much as in *R. campestris*, by the antero-superior integumental web.

Since the hind foot was of a more rusty tawny hue than the front foot, and measured half an inch more from the fetlock to the tip of the hoof, there can be very little doubt that it belonged to a different species or subspecies, possibly to a different genus, of Antelope. Considering the differences the two feet present from those of *R. campestris*, the evidence is, I think, in favour of their belonging to the genera *Neotragus* or *Nesotragus*, perhaps one to *moschatus* and the other to *livingstonianus*.

*Nototragus*\* *melanotis* Thunb. (the Grysbok) has, according to Owen, preorbital and inguinal glands. Max Weber, however, says that although the preorbital gland ("Thränengrube") is present in the male, in the female it is represented by a naked area of skin. This statement must be taken with reserve, in my opinion, since it does not appear to have been based upon fresh material (see under *Ourebia ourebi*). I have not examined material of this species.

Genus OUREBIA Laurill.

OUREBIA OUREBI Zimm. (= *scoparia* Schr.).

(The Cape Oribi.)

According to Owen, this species has large preorbital glands and inguinal pits. Max Weber, on the contrary, states that, although the male has a deep preorbital gland, this organ is apparently represented in the female by a naked spot in front of the eyes. This observation must, I think, have been made upon a mounted specimen, for I cannot reconcile it with the fact that in the female of *O. nigricaudata* described below, and in one of *O. montana*, now living in the Gardens, the preorbital gland is well developed and valvular.

OUREBIA NIGRICAUDATA Brooke.

(The Black-tailed Oribi.) (Text-figs. 99, 100.)

I have seen two young examples, male and female, of this species from Senegambia, presented by Sir George Denton. The preorbital gland was marked externally by a longish slit running downwards from a point close to the anterior angle of the eye. This was capable of considerable distension, and led into a simple pocket-like invagination dipping into a large, oval, black, glandular mass. Under pressure, the secretion, black and adhesive like lamp-black, could be squeezed from two areas marked by depressions, one near the middle, the other upon the upper corner of the gland. Each depression contained several pores, from which long coiling threads of the substance exuded. The gland and its orifice were relatively longer in the male than in the female.

The so-called glandular patch beneath the ear was rather scantily clothed with very short hairs. In section the skin was seen to be markedly thinner than that of the surrounding area, and showed no evidence of specially developed glands.

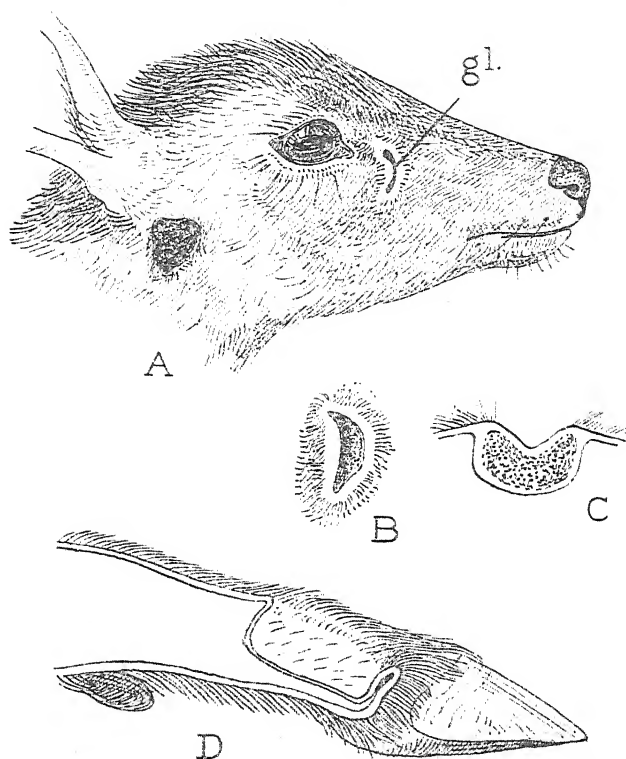
There were two pairs of teats.

The inguinal glands were represented in the female by a pair of

\* This generic name was proposed by Thomas and Schwann for the Grysbok (Abstr. P. Z. S. No. 27, p. 10, 1906), because it differs from *Rhaphicerus* in possessing supplementary hoofs. Mr. Lydekker's statement, therefore, that the genus was based upon *R. campestris* (the Steinbok), which has no supplementary hoofs, is erroneous ('The Game Animals of Africa,' p. 181, 1908).

shallow depressions, each marked by a tuft of hair arranged in a whorl and situated in the ordinary position near the mammæ. In the male, however, they were far back alongside the scrotum, a very unusual position. Each consisted of a short sac, with tumid orifice, whence a large tuft of hairs protruded.

Text-fig. 99

*Ourechia nigricaudata* ♀.

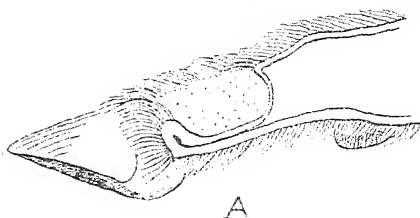
- A. Head to show orifice of preorbital gland (*gl.*) and nearly naked patch below ear.
- B. Preorbital gland with orifice distended.
- C. Section of preorbital gland.
- D. Median vertical section of front foot. (N.B. The hairs within the cleft are too long, coarse, and clearly defined.)

The tuft of hairs below the knees covered an area of thickened integument as in Gazelles. There were no special indications of glandular activity, however, beyond a certain amount of powdery scurf at the base of the long hairs.

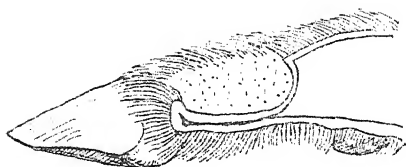


The pedal glands, present on all four feet, were very like those of Gazelles, except that the fold of skin forming the heel-tie

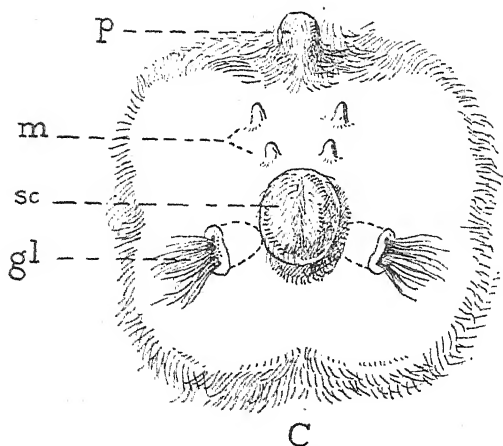
Text-fig. 100.



A



B



C

*Onurebia nigricaudata* ♂.

A. Median vertical section of front foot.

B. The same of hind foot.

C. Inguinal region: *p.*, penis; *m.*, mammae; *sc.*, scrotum; *gl.*, inguinal gland with tuft of hair protruding from the orifice.

extended less to the front, so that the cavity of the interdigital cleft was to a greater extent in communication with the space

between the hoofs. This was more marked in the male than in the female, and in the former sex the heel-tie was thinner and less produced in the hind than in the front leg. The walls of the glandular interdigital depression were scantily covered with short hairs; but the heel-tie itself was thickly clothed with long hairs, largely overlapping the base of the hoofs on their inner aspect. The chief difference between the feet of this species and those of *Raphicerus campestris* lies in the fact that the interdigital cleft is not overlapped above by a long integumental fold, and that the fold of skin along the back of the pastern extends right down to the heels, tying them together, and extends further forwards towards the anterior edge of the hoofs. From this arrangement it comes about that the hoofs of *Ourebia* are much less distensible than in *Raphicerus*; they are also shorter: the combination of these two features suggesting that *Ourebia* habitually frequents harder ground.

The structure of the feet in *Ourebia*, correlated with that of the preorbital glands and the presence of well-developed tufted carpal or knee glands and of a single pair of inguinal glands, is strongly suggestive of affinity between that genus and *Gazella*.

By the structure of the feet, *Ourebia* and *Raphicerus* may be distinguished as follows:—

- |  |                    |
|--|--------------------|
| a. Orifice of glandular interdigital cleft much shorter than the cleft itself, which is partially overlapped in front and above by a longish integumental fold or web; posterior web of the pastern not reaching the heels, which can thus be widely separated.....  | <i>Raphicerus.</i> |
| a'. Orifice of glandular interdigital cleft approximately as long as the cleft itself, which is not to any appreciable extent overlapped above and in front by an integumental fold; posterior web of the pastern reaching the heels, which are thus capable of being separated only to a very limited extent..... | <i>Ourebia.</i>    |

#### Subfamily OREOTRAGINÆ.

#### Genus OREOTRAGUS H. Sm.

OREOTRAGUS OREOTRAGUS Zimm. (The Klipspringer.)

(Text-fig. 101, A, B.)

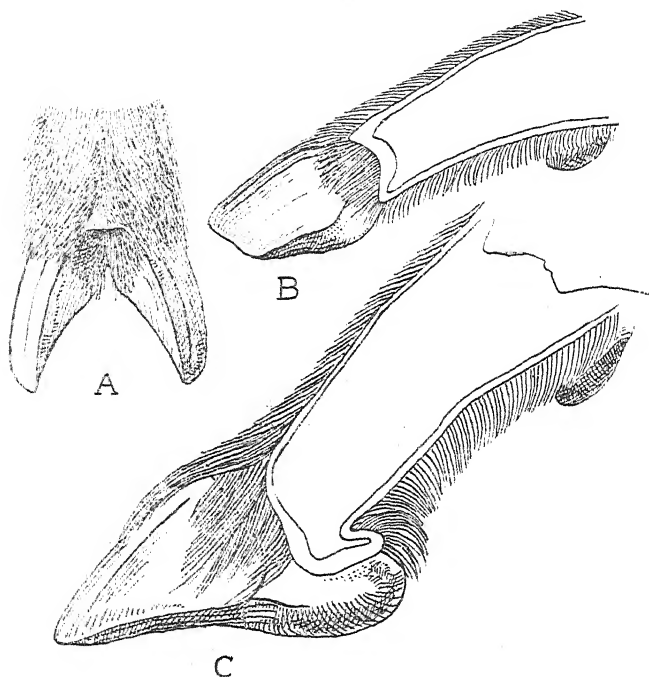
According to Owen, this species has preorbital glands but no inguinal pits. H. Smith, on the contrary, says that inguinal glands are present.

In a foot of this species, given to me by Rowland Ward, which had the bones of the pastern cut away from behind, but with the skin of the interungual area and of the front of the pastern entire, I could find no trace of pedal gland. The skin on the middle line of the pastern in front showed no sign of depression. Stopping short a little above the proximal margin of the hoof, it turned sharply backwards at right angles between the hoofs to

form the interungual web, which in section was shown to be thick and horny and to meet that of the back of the pastern just above the heels.

Thus the foot of this genus differs essentially from that of the genera of *Neotraginæ* above described, in that the integument of the back of the pastern is not folded back upon itself to form the posterior wall of an interdigital cleft or depression. But, as in

Text-fig. 101.



- A. Anterior view of pastern of *Oreotragus oreotragus* (? of front or hind foot) with hoofs distended.
- B. Median vertical section of the same foot.
- C. The same of front foot of *Pantholops hodgsoni*.

the *Neotraginæ*, the interungual area is covered with long hairs from the front of the pastern to the back, there being merely a small triangular naked spot at the summit of the interungual web. In spite of the thickness and strength of this web, the hoofs can be widely separated and, as is well known, their points are very broad and truncated, the animal resting upon these truncated extremities instead of on the heels.

## Subfamily ANTILOPINÆ.

Genus GAZELLA Licht. (Text-figs. 102, 103; 104, A-C.)

According to Owen, the following species of *Gazella* have large preorbital glands and inguinal pits:—*G. dorcas*, *subgutturosa*, *bennettii*, *arabica*, *sæmmeringii*, *mhorr*, *ruficollis*, *rufifrons* (*kevella*)\*. With these he contrasts *colus* and *gutturosa* as having small preorbital glands.

Ogilby states that this genus has distinct and movable preorbital glands, very large pedal and inguinal glands, and one pair of mammae.

Hodgson examined *G. dorcas* and *G. bennettii*. He correctly says of the former that it possesses distinct preorbital glands, large pedal glands on all four feet, and large and distinct inguinal glands. Of *G. bennettii*, on the contrary, he asserts that the preorbital glands are absent, and he consequently erected the genus *Tragops* for its reception. Blanford and others, however, say that these glands are present in *G. bennettii*, an observation quite in accord with my own.

Of the genus *Gazella* I have examined one or more specimens of the following species:—

*G. bennettii*. Several examples of both sexes, mostly from Persia.

*G. subgutturosa*. One male and one female from Meshed.

*G. marica*. Two males from Central Arabia.

*G. muscatensis*. Several specimens from South Arabia.

*G. dorcas*. An adult pair from Egypt.

*G. pelzelni* (?). One quite young female from Somaliland.

*G. cuvieri*. One old female from Morocco.

*G. rufifrons*. One young male from Senegal.

*G. sæmmeringii*. One skin of an adult male lent by Mr. E. Gerrard.

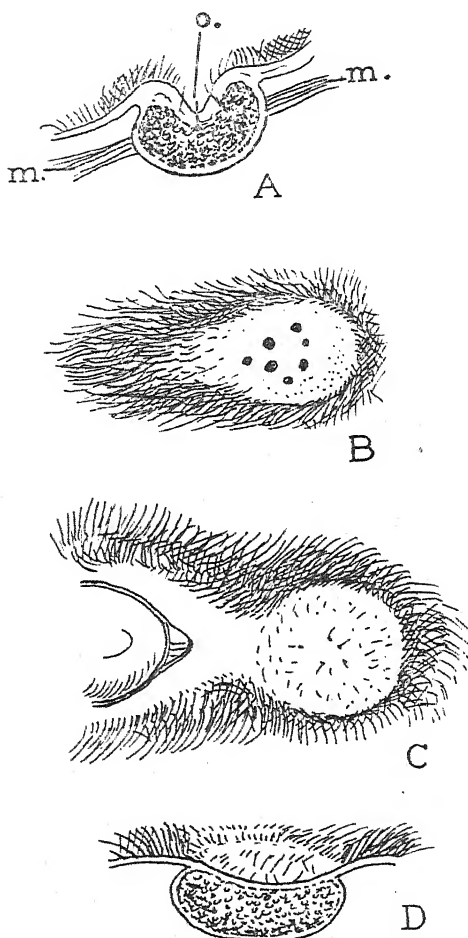
So constant in structure and occurrence are all the glands that a detailed description of them, as exhibited by each species, is unnecessary.

The preorbital gland is valvular. When closed it has the form of a vertical slit of black nearly hairless skin extending downwards from a point a little in front of the anterior corner of the eye. When opened to its fullest extent, it appears as a subcircular patch of skin, scantily beset with short hairs, and marked with a shallow central depression, which is, in reality, the bottom of the invaginated pocket. The gland itself, when extracted from the preorbital pit of the skull, is seen to consist of a black integumental thickening formed round the invagination. In the case of *G. dorcas* I found that the inner surface of the pocket had about seven large holes, from which, under pressure,

\* I infer that *rufifrons* is the species cited by Owen under the name "*kevella*," because he gives Senegal as its locality.

secretion could be squeezed first in the form of black waxy threads, then as fluid drops, the waxy consistency being due, I expect, to the pores being blocked and inoperative for some little time before

Text-fig. 102.



- A. Section of preorbital gland of *Gazella dorcas*: o., orifice of gland  
m., muscle.  
B. Superficial view of the same gland flattened.  
C. Superficial view of the flattened preorbital gland of *G. cuvieri* ♀.  
D. The same gland in section.

death. Fluid drops could also be squeezed from the hair-pores studding the surface of the integument. The secretion contained

in the pocket itself is black and sticky. It may here be mentioned that Ogilby long ago (P. Z. S. 1836, p. 38) described the preorbital gland of a Gazelle as being furnished with six excretory ducts placed nearly in a circle and with one central duct, from the orifices of which there issued strings of a dense ceruminous matter.

The inguinal glands are always two in number, consisting of deeper or shallower pouches opening by larger or smaller orifices situated just externally to the mammae. The pouches dip into a mass of vascular tissue just above the mammae. They are usually about one inch deep and about as wide inside as deep or a little wider, the integument surrounding the orifice and the mamma being naked. In a male *G. subgutturosa* the orifice was nearly as large in diameter as the scrotum; in *G. dorcas* and *G. muscatensis* it was considerably smaller and the lumen of the pouch was correspondingly smaller in the two latter than in the former. The largest gland of all was found in the female of *G. cuvieri*, in which it was two inches deep and about twice as deep as wide, and as wide at the orifice as within.

The walls of the pocket were, in all cases, sparsely covered with short hairs, and the secretion was waxy and drier at the orifice than at the bottom of the pouch. It has a very strong odour. In *G. bennettii* and *subgutturosa* it is yellow in colour and smells exactly like the urine of the common House Mouse (*Mus musculus*); in *G. cuvieri* the colour is greenish yellow and the smell a mixture of mouse urine and flour-paste.

In a female of *G. dorcas* the inguinal gland secretion was pale green and resembled in scent a mixture of flour-paste and cheese; the pedal glands had a strong and decided, but peculiar and indescribable, smell; the secretion of the knee glands had a repulsive odour of dogs' dung, while that of the preorbital glands, although faint and quite indescribable, was not unpleasant. This specimen furnished an admirable instance of the fact below alluded to, that scents of totally different character may emanate from the glands of one and the same individual. This was further borne out by a specimen of *G. muscatensis*, in which the green secretion of the inguinal glands smelt exactly like cream-cheese, that of the knee gland like a Domesticated Sheep, while the pedal glands had a faint and indescribable, but different odour from either.

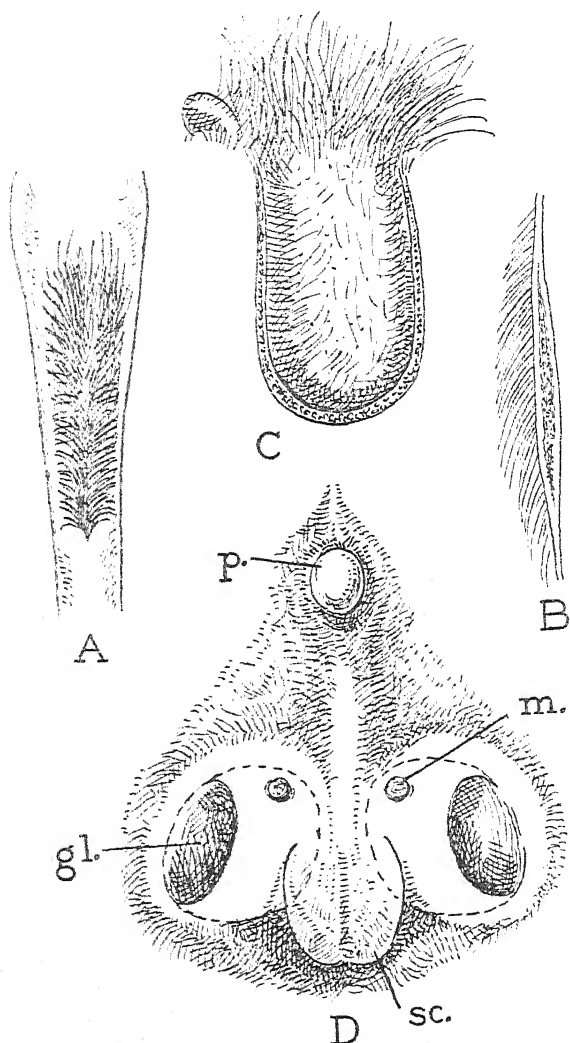
It may be noted in passing that the smell of the inguinal secretion in specimens of *G. bennettii* and *G. subgutturosa* from Persia is the same as that of *Ovis vignei* from the same country.

Although there is typically only a single pair of mammae in Gazelles, now and again there are two pairs, indicating, no doubt, the descent of these animals from quadrimammate ancestors. Similar atavism is sometimes seen in Sheep. When there are two pairs in Gazelles, the inguinal glands are connected with the posterior pair, showing that the anterior pair are supernumerary.

The pedal glands are well and equally developed on all four feet. When the hoofs are together, the orifice has the form of a narrow

slit dividing the hairs on the front of the pastern. When the hoofs are forcibly distended, it appears as a triangular cleft, pointed

Text-fig. 103.



- A. Superficial view of knee gland of *Gazella dorcas*.
- B. Longitudinal section of the same.
- C. Transverse section of inguinal gland of *G. cuvieri* ♀.
- D. Inguinal region of *G. subgutturosa*: p., penis; m., mamma; sc., scrotum; gl., orifice of inguinal gland, its area beneath the skin shown by dotted line.

above and wide below, above the base of the hoofs. The summit of the cleft is arched over to a small extent by a slight web of integument, and the bottom of it is closed by a strong and deep web which passes forwards from the heels of the hoofs to a point nearly on a level with their proximal edge in front. This web firmly ties the hoofs together, so that, in a living animal standing naturally, they never splay apart like those of Sheep and Goats, although when it rears up against anything the front hoofs often spread to a considerable extent. The skin forming the interungual web is folded sharply upon itself in front and passes back to the heels; its inner layer thence passes upwards only a little in front of the skin of the back of the pastern, then curves forwards about on a level with the joint between the penultimate and antepenultimate phalanges to meet the skin of the front of the pastern in the small web described above, thus forming the bottom, back, and top of the long interdigital cleft, the orifice of which is almost as long as the cleft itself. The walls of the cleft are only sparsely covered with short hairs; and I have never detected any signs of secretion either on them or on the longer hairs fringing the edges of the orifice or on the tufts of still longer hairs overhanging the proximal portion of the hoofs in front.

The interungual web is continuously hairy from front to back, though the hairs often become somewhat thinner towards the heels. The latter are well developed, and the hoofs are never long, though in these two particulars they are not specialised to the same extent as in Goats and Sheep, which stand rather more upright than Gazelles.

Dr. Murie long ago pointed out that the knee-tufts of *Saiga* are glandular. Mr. Lydekker made the same suggestion with regard to Gazelles ('Field,' March 14, 1908). This suggestion proves to be correct. The hairs are directed downwards, those on each side of the middle line usually crossing at the tips, somewhat as in the metatarsal gland of the Impala (*Epyceros melampus*). The underlying skin is much thicker than that of the rest of the leg; but the thickening, accompanied by increase in size of the sebaceous glands, is not abrupt but gradual, thinning away into the normal skin all round the circumference of the area. The hairs covering the latter hold a quantity of scurfy secretion.

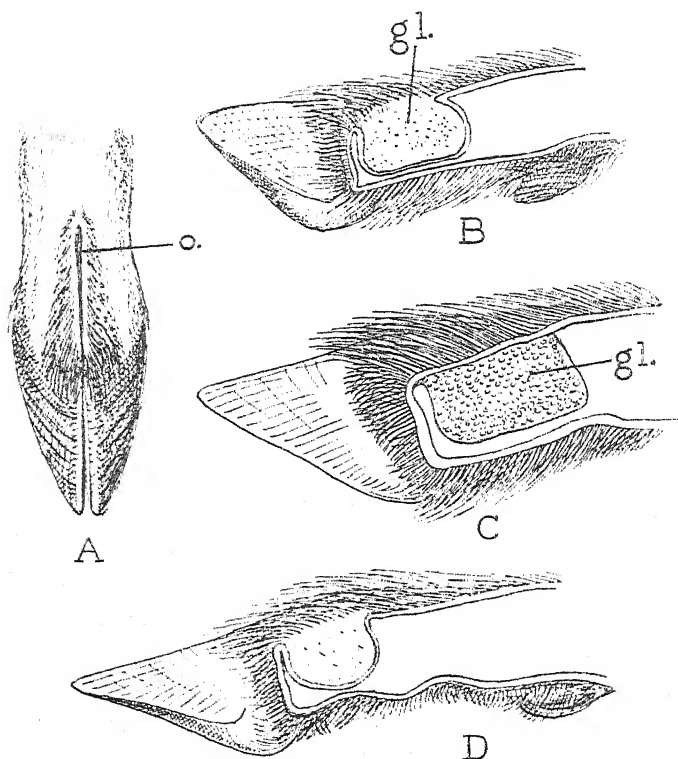
As a general rule, the knee-glands are covered with long hairs forming a continuous pad and not showing, when undisturbed, any central longitudinal line; but in three examples of *G. dama ruficollis*, now living in the Gardens, the hairs are quite short and their inwardly directed tips do not meet in the middle line, so that the median gutter is plainly visible.

According to Hodgson the Tibetan species of Gazelle known as *picticaudata* has no preorbital or inguinal glands and has small pedal glands on all four feet. If his account be trustworthy, the species differs from all the true Gazelles I have examined in the absence of the preorbital and inguinal glands, not to mention the



seemingly smaller size of the pedal glands. Hodgson erected the genus *Procapra* for *picticaudata*; and, in view of the constancy in occurrence and development of the cutaneous glands in the species of *Gazella* I have examined, I am disposed to think that *Procapra* should be admitted as a valid genus, comprising probably, in addition to *picticaudata*, *gutturosa* and *przewalskii*. I do not know whether these three species are in actual agreement as regards cutaneous glands; but they at least differ from all the southern species of *Gazelles* in the shortness of the tail.

Text-fig. 104.



- A. Hind foot of *Gazella subgutturosa* showing slit-like orifice of pedal gland (o.).  
 B. Median vertical section of front foot of *G. bennettii*: gl., glandular cleft.  
 C. Foot of *G. eurieri* dissected to show the gland *in situ*.  
 D. Median vertical section of foot of *Antidoreas marsupialis*.

The validity of *Procapra* was discussed by Messrs. Sclater and Thomas ('Book of Antelopes,' iii. p. 73), and the claims of the genus to recognition were dismissed on the grounds that three of the characters in which the above-mentioned species agree (namely,

the absence of knee-tufts, of preorbital glands, and of horns in the female) are not absolutely distinctive of the group; *G. subgutturosa*, for instance, has the female hornless and "several species besides [the three in question] are without knee-brushes, while the antorbital fosse in others are so shallow as to be practically non-existent." In accordance, however, with the modern more restricted application of generic names, it may be doubted whether these reasons will be regarded as invalidating *Procapra* from recognition, especially as the shortness of the tail seems to be an absolutely distinctive feature of the three above-mentioned species, as compared with Gazelles proper.

Pallas, according to Gray \*, says that the male of *G. gutturosa* has a follicle, like the musk-bag of *Moschus*, in front of the prepuce. Still more interesting is the record by Hodgson of the presence of a large sinus behind the horns in *picticaudata*. This probably represents the postcornual gland of *Rupicapra*. Indeed, four of the characters cited by Hodgson as diagnostic of *Procapra*, namely, the absence of preorbital glands and of inguinal glands, the presence of small pedal glands, as compared with those of *Gazella*, on all four feet, and of a postcornual sinus, apply equally well to *Rupicapra*; and it may be that in *P. picticaudata* we have the link between *Rupicapra* and *Gazella*. Possibly also the organisation of *Procapra* may throw some light upon the true position of *Saiga* and *Pantholops*.

#### Genus ANTIDORCAS Sund.

ANTIDORCAS MARSUPIALIS Zimm. (= *euchore*).

(The Springbuck.) (Text-fig. 104, D.)

According to Owen, this species, which he appears to quote twice, under the names *Antilope euchore* and *pygarga*, has large preorbital glands and inguinal glands.

No information as to the glands is contained either in Slater and Thomas's 'Book of Antelopes,' or in W. L. Slater's volume on 'The Mammals of S. Africa,' or in Rowland Ward's 'Great and Small Game of Africa.'

I have examined three examples of this species, two males and a female. The preorbital glands resemble those of the Gazelles described above, except that the gland itself is pale yellow instead of black in colour. When everted and squeezed, the gland yields a clear fluid.

In spite of what Owen says, there is no trace of inguinal glands.

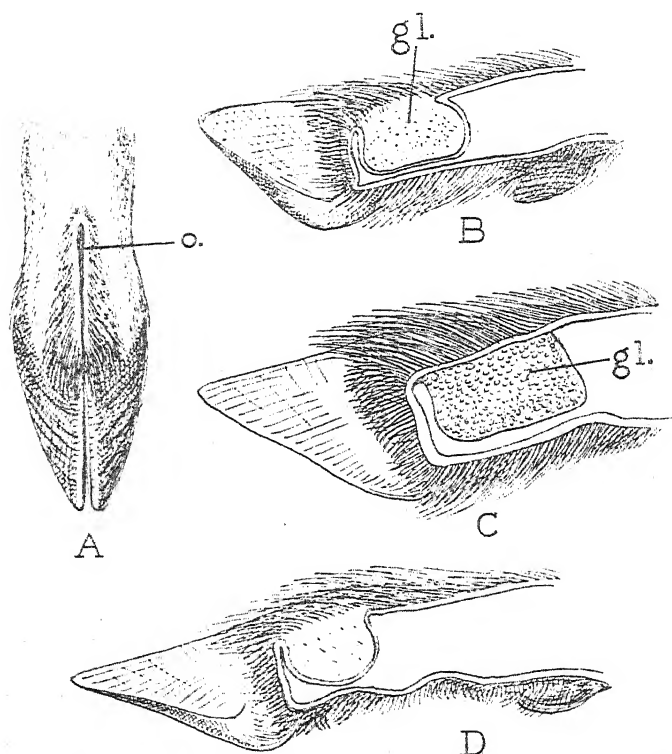
Pedal glands are present on all four feet and so closely resemble those of Gazelles as to need no redescription.

There are no knee glands, the knee-tufts being absent, as has already been recorded by previous describers.

\* Cat. Rum. Mamm. in B. M. p. 37, 1872.

seemingly smaller size of the pedal glands. Hodgson erected the genus *Procapra* for *picticaudata*; and, in view of the constancy in occurrence and development of the cutaneous glands in the species of *Gazella* I have examined, I am disposed to think that *Procapra* should be admitted as a valid genus, comprising probably, in addition to *picticaudata*, *gutturosa* and *przewalskii*. I do not know whether these three species are in actual agreement as regards cutaneous glands; but they at least differ from all the southern species of *Gazelles* in the shortness of the tail.

Text-fig. 104.



- A. Hind foot of *Gazella subgutturosa* showing slit-like orifice of pedal gland (o.).  
 B. Median vertical section of front foot of *G. bennettii*: gl., glandular cleft.  
 C. Foot of *G. curvieri* dissected to show the gland in situ.  
 D. Median vertical section of foot of *Antidorcas marsupialis*.

The validity of *Procapra* was discussed by Messrs. Sclater and Thomas ('Book of Antelopes,' iii. p. 73), and the claims of the genus to recognition were dismissed on the grounds that three of the characters in which the above-mentioned species agree (namely,

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#### Genus ANTIDORCAS Sund.

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(The Springbuck.) (Text-fig. 104, D.)

According to Owen, this species, which he appears to quote twice, under the names *Antilope euchore* and *pygarga*, has large preorbital glands and inguinal glands.

No information as to the glands is contained either in Sclater and Thomas's 'Book of Antelopes,' or in W. L. Sclater's volume on 'The Mammals of S. Africa,' or in Rowland Ward's 'Great and Small Game of Africa.'

I have examined three examples of this species, two males and a female. The preorbital glands resemble those of the *Gazelles* described above, except that the gland itself is pale yellow instead of black in colour. When everted and squeezed, the gland yields a clear fluid.

In spite of what Owen says, there is no trace of inguinal glands.

Pedal glands are present on all four feet and so closely resemble those of *Gazelles* as to need no redescription.

There are no knee glands, the knee-tufts being absent, as has already been recorded by previous describers.

\* Cat. Rum. Mamm. in B. M. p. 37, 1872.

To compensate, as it were, for the absence of inguinal and knee glands, the Springbuck has an immense dorsal gland, the skin underlying the well-known white dorsal shield having highly developed sebaceous glands secreting a yellow sticky substance which stains the bases of the white hairs yellow or forms a scurfy kind of powder about their roots. No such substance is found upon the hairs of the rest of the back; and the skin of the area in question has a markedly fatty appearance when stripped, its colour differentiating it at once from that of the shoulders and sides of the body. Mr. F. E. Beddard, F.R.S., long ago noticed the glandular nature of this patch and drew my attention to it.

#### Genus ANTILOPE Pall.

ANTILOPE CERVICAPRA Pall. (The Indian Blackbuck).

(Text-fig. 105, A-C.)

The large size of the preorbital gland in this species has attracted the attention of zoologists from early times. The presence of inguinal glands was recorded by Owen in 1836 and independently in the same year by Ogilby, who stated at the same time that there are large pedal glands and only one pair of mammae. These observations were repeated by Hodgson and have been copied by recent systematic authors.

Through Mr. Herbert Bolton, F.R.S.E., F.Z.S., I am indebted to the Committee of the Bristol Museum for the stuffed skin of a male of this species, and Mr. Gerrard kindly supplied me with another.

Mr. Gerrard's specimen had the preorbital glands intact and by cutting them I was able to see that they differed in no essential particulars from those of Gazelles, except that they were very much larger, the infolding forming a long deep hair-lined space, and the glandular portion being very thick and pale in colour. The structure and general features of this organ have already been described by Bennett, Owen, and others.

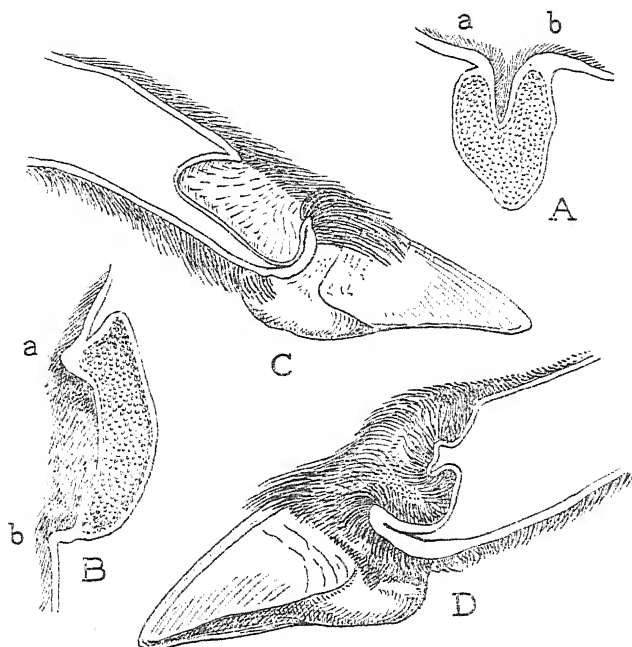
The orifices of the inguinal glands were clearly shown opening close to the mammae, of which there was a single pair.

The pedal glands were present in all four feet and were very like those of Gazelles. The walls of the interdigital cleft were furnished with longer hairs; the interungual integument was much thicker and more horny, forming a stronger tie between the hoofs; its anterior extremity was slightly recurved and furnished with a somewhat radiating tuft of hairs, the longest of which overhung the proximal edge of the hoof in front, while between this tuft and the heel-tie the skin was naked. There was no naked horny pad on the knees: but the knee gland was developed as in Gazelles, the roots of the long hairs being packed with scurf-like secretion.

The number, position, and structure of the cutaneous glands show close relationship between the genera *Antilope* and *Gazella*,

the only difference I can find between the two being the thickness, smoothness, and curvature of the interungual integument.

Text-fig. 105.



- A. Transverse section of preorbital gland of *Antilope cervicapra* ♂ :  
 a, skin extending towards the eye ; b, towards the nose.  
 B. Vertical or longitudinal section of the same gland : a, upper, b, lower  
 extremity.  
 C. Median vertical section of front foot of *Antilope cervicapra*.  
 D. The same of hind foot of *Lithocranius walleri*. (The fold in the integument of the wall of the gland probably absent in fresh specimen.)

In a living male specimen of this species the secretion of the inguinal glands smells exactly like flour-paste and might be described as starchy. The secretion of the preorbital gland is peculiar and indescribable. I cannot agree, however, with Bennett that the odour is urinous\*.

\* It is not, I believe, generally known to naturalists and sportsmen, though the fact is perhaps familiar to some who have paid attention to animals in captivity, that the adult male of this species undergoes a marked seasonal change of colour. During the summer months, that is to say, from about May to August, the colour, except of the face, is like that of females and young males, namely tawny. In the latter part of August or thereabouts, the coat begins to darken and gradually but rapidly assumes the dark hue whence the trivial name of the species "Blackbuck" has been derived. At or about the beginning of May the opposite change rapidly

Genus *LITHOCRANIUS* Kohl.*LITHOCRANIUS WALLERI* Brooke.

(The Gerenook or Waller's Gazelle.) (Text-fig. 105, D, p. 895.)

No fresh material of this species has been available for examination.

Elliot describes the preorbital gland as a "conspicuous prominence with a central aperture, from which exudes a black secretion that stains everything it touches in the same way that ink does"\*. Judging from this description the gland is better developed than in Gazelles, but the colour of the secretion appears to be the same.

On a fore and a hind foot kindly lent to me by Mr. Edward Gerard I have found well-developed pedal glands, each consisting of a large saccular invagination on the front of the pastern. The orifice is as large as in Gazelles, and extends up the pastern as far as the joint between the penultimate and the antepenultimate phalanges. The inferior edge of the orifice is formed as in Gazelles by the interungual web, which, however, differs from that of Gazelles in passing only halfway along the space between the heels and the anterior proximal margin of the hoof. It is also much thicker and more horny than in Gazelles; but, as in the latter, is folded upon itself to form in the same way the back and upper wall of the glandular interdigital cleft. In the specimen examined, this wall was thrown into folds, suggesting a sac too voluminous for the space containing it. The walls of the gland were clothed with longish hairs, all projecting forwards or downwards towards the margins of the orifice, a downwardly directed fringe of hairs clothing the edge of the interungual web.

The entire pastern is clothed with very short close-set hair, with a small black tuft over the proximal end of the hoof in front; a felting of thick close-set hair clothes the integument on the inner surface of the hoof above the proximal margin of the nail and of the heels.

The hoofs are longer than in Gazelles, and capable of greater distension, on account of the web being shorter and situated somewhat higher above the hoofs.

Although the pedal glands of this genus are more like those

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takes place, the first sign of it being a gradual lightening along the middle of the back. In August, when the blackening sets in, it appears first most pronouncedly upon the neck, legs, and fore quarters, and gradually spreads backwards.

For three consecutive years I have observed this in a specimen in our Gardens. I do not know what theory Indian sportsmen hold as to the disappearance of "Blackbucks" from the herds during the months they are in "eclipse" pelage, to borrow an ornithological expression. But, since most of them, I imagine, believe all tawny individuals to be does or young bucks, they must suppose, I conceive, that the adult bucks have separated themselves from their companions, an inference clearly not justified by the facts.

\* 'Great and Small Game of Africa,' p. 371, 1899 (Rowland Ward).

of the Gazelles above described than they are like the glands of any other Antelope, they present well-marked differences from them.

There was a well-developed knee-pad of black and reddish hairs much longer than those of the surrounding skin and stuck together with plentiful dry secretion.

On skins of this genus in the British Museum I found two pairs of teats, but no evidence of inguinal glands.

As attested by other characters, this genus is an aberrant type most nearly allied to *Gazella*; but in the structure of the feet it seems to be less closely related to *Gazella* than is *Antilope* or *Antidorcas*. I do not feel sure, however, that the shape of the upper wall of the interdigital cleft in the example described and figured was not due to mutilation, since the skin of the pastern had been cut away at the back, perhaps thus loosening the connective tissue which normally holds the invaginated sac in place. It is very desirable that fresh examples of this species be examined.

Excluding *Procapra*, which I have not seen, the genera here referred to the Antilopinae may be distinguished as follows by the structure of the feet and by their cutaneous glands:—

- |  |                       |
|--|-----------------------|
| a. An immense dorsal gland extending from the middle of the back to the rump, feet, and preorbital gland approximately as in <i>Gazella</i> , but no inguinal glands .....                   | <i>Antidorcas</i> .   |
| a'. No dorsal gland.   |                       |
| b. Feet with the folded interungual web extending only a little more than halfway between the heels and the proximal edge of the hoof in front; no inguinal glands; two pairs of mammae..... | <i>Lithocranius</i> . |
| b'. The folded interungual integument extending forwards nearly to the proximal margin of the hoof in front; a pair of inguinal glands; normally a single pair of mammae.                    |                       |
| c. Interungual integument thinner, hairy, the interdigital cleft practically naked .....   | <i>Gazella</i> .      |
| c'. Interungual web smooth; interdigital cleft more hairy...   | <i>Antilope</i> .     |

In addition to the four genera just described, the Antilopinae, according to accepted views, comprises the genera *Dorcotragus*, *Ammodorcas*, *Pantholops*, *Saiga*, and *Epyceros*. I do not, however, think these can be included in the subfamily without unwarrantably upsetting its homogeneity. Kinship is possible between *Ammodorcas* and *Epyceros* on the one hand and between *Saiga* and *Pantholops* on the other, but it does not appear to me that the two latter have any close relationship with the two former; it is indeed very far from obvious why the genera should be associated in the pairs suggested. Pending the demonstration of relationship such as would justify such a course, I propose to relegate *Pantholops*, *Saiga*, and *Epyceros* each to its own subfamily and to leave *Ammodorcas* for the present unplaced. In the following pages *Ammodorcas* will be found near the Cervicaprinae (p. 917). It may be added that these four genera differ widely in the structure of the feet from those here restricted to the Antilopinae.



## Subfamily SAIGINÆ.

## Genus SAIGA Gray.

## SAIGA TARTARICA Linn. (The Saiga.)

According to Dr. Murie (P. Z. S. 1870, p. 500) this animal has a pair of small preorbital glandular pits; a pair of carpal or knee glands; a pair of shallow inguinal pouches in one specimen examined, but not in another, a younger example, although the secretory area was very evident; and pedal glands in all four feet. These are described as "about  $1\frac{1}{2}$  inch in depth and opening by a narrow constricted aperture" at the "front and upper part" of the foot. Although on p. 502 of this memoir Dr. Murie remarks that these glands "hardly form satisfactory grounds for basing affinity upon," it is nevertheless quite clear from his description of the pedal glands that they are much more like those of a Sheep than of a Gazelle or Black-buck. The description is not sufficiently detailed to permit the conclusion that the pedal glands exactly resemble those of *Ovis*; but it is quite certain that with their narrow constricted orifice they bear no similarity to the long interdigital cleft of *Gazella* or *Antelope*. Their structure, in fact, bears out Dr. Murie's opinion that the Saiga may be regarded as an Antelopine Sheep.

In any case, it seems evident that the genus is an isolated one. I think, therefore, that it should form, provisionally at all events, the type of a special subfamily.

## Subfamily PANTHOLOPINÆ.

## Genus PANTHOLOPS Hodg.

## PANTHOLOPS HODGSONI Abel. (The Chiru.)

(Text-fig. 101, C, p. 886.)

In 1836 Hodgson (P. Z. S. 1836, p. 39) described the inguinal glands as "exceedingly large sacs which hang by a long narrow neck from the groin." He re-affirmed the same fact in other words in his paper in 1847, where he adds that preorbital glands are absent, but the pedal glands are present and large on all four feet. Blanford and Lydekker repeat his observations, without alluding to the pendent inguinal glands, while the latter supplements his account with Kinloch's observation that these glands penetrate a considerable distance into the body.

Hodgson's statement as to the pendulous nature of the inguinal glands is puzzling. It is hardly likely that they can be voluntarily eversible and retractile, and I can only suppose that he saw them hanging as loose sacs on a stripped skin.

The only material of this species I have been able to examine fully was a mounted head and two feet, fore and hind, of a male specimen, for which my best thanks are due to Mr. Edward

Gerrard, and a single foot shown by its colour to be that of a female, which was kindly given to me by Messrs. Rowland Ward, Ltd.

The head enabled me to confirm Hodgson's statement as to the absence of the preorbital gland, and the feet to refute his statement as to the presence of the pedal glands—they are absent. The integument along the middle line of the pastern forms a very shallow depression. Near the proximal end of the hoof in front it turns backwards at a rounded angle and runs almost parallel to the inner proximal margin of the nail to the heels, joining them together throughout their length. The posterior portion of the heels is well developed and the skin which unites them behind is folded sharply upon itself for a short distance, then turns up to be continuous with the skin of the back of the pastern. The back of the pastern and the fold in question are thickly hairy, and the interungual integument or web is covered with long hairs as far down as the point where the heel-tie begins. These hairs are especially long at the base of the hoof in front, and overhang the anterior edge of the nail nearly to its tip. Thus the integumental web which ties the hoofs together is as deep and strong as in Cattle (*Bos*) or Elands (*Taurotragus*), and the feet are quite different from those of typical Gazelles, to which *Pantholops* is usually held to be closely related; and the hoofs clearly have nothing like the power of extension seen in the feet of Sheep and Goats.

According to Hodgson, there is only a single pair of mammae, and I only succeeded in finding one pair in a dried skin of a male in the British Museum. I noticed in this skin that the orifice of the inguinal gland on each side lies some four or five inches away from the teat. On one side the gland was loose or pendent, as Hodgson described it; but on the other it was adherent and directed inwards from the orifice as a slightly expanding tube, its inner extremity lying close to the teat. This, no doubt, is its natural position, judging from the direction of the gland in other Bovidae that possess it.

In 1872 Gray recognised the peculiarities of this genus by placing it in a special family, *Pantholopidae*.

*Saiga* is commonly held to be related to *Pantholops*, perhaps correctly; but the relationship is not close. Apart from the well-known differences between them in the structure of the skull and nose, they may be distinguished as follows:—

- |   |                    |
|---|--------------------|
| a. Pedal glands, apparently ovine, on all four feet; preorbital glands present; inguinal glands small and close to the mammae, of which there are two pairs .....   | <i>Saiga.</i>      |
| a'. No trace of pedal glands; no preorbital glands; inguinal glands very large and deep, with orifice remote from the mammae, of which there is a single pair ..... | <i>Pantholops.</i> |

In the characters here used, however, the two genera do not differ from each other much more than *Ovis* differs from *Pseudois* or *Capra*.

## Subfamily BUBALINÆ.

## (Hartebeests and Gnus.)

Of this group Owen records the presence of preorbital glands and the absence of inguinal glands in the following species:—*Damaliscus lunatus*, *Bubalis boselaphus* (= *Antilope bubalis*), *B. caama*, *Gorgon taurinus*, and *Connochætes gnu*.

Ogilby, who examined *Bubalis boselaphus*, which he quotes as *B. mauretanicus*, confirms Owen's statement regarding the above-given particulars, adding that the pedal glands are large and that there is a single pair of mammae.

Recent systematic writers agree with Ogilby as to the number of mammae; but in spite of his use of the epithets "*exigui, distincti*" in describing the preorbital glands, these are quite commonly, but erroneously, stated to be small.

Of Hartebeests belonging to the genus *Bubalis* I have seen no complete material, and have been compelled to rely upon soaked feet and masks usually with the skin only of the preorbital gland retained. Of the White-tailed Gnu (*Connochætes gnu*) I have seen two freshly dead specimens. I have, however, seen living examples of the two species of Gnu (*G. taurinus*, *C. gnu*) and of two species of *Damaliscus* (*D. pygarga* and *D. albifrons*, the Bontebok and Blesbok respectively).

## Genus BUBALIS Frisch.

## BUBALIS CAAMA F. Cuv. (Text-fig. 106.)

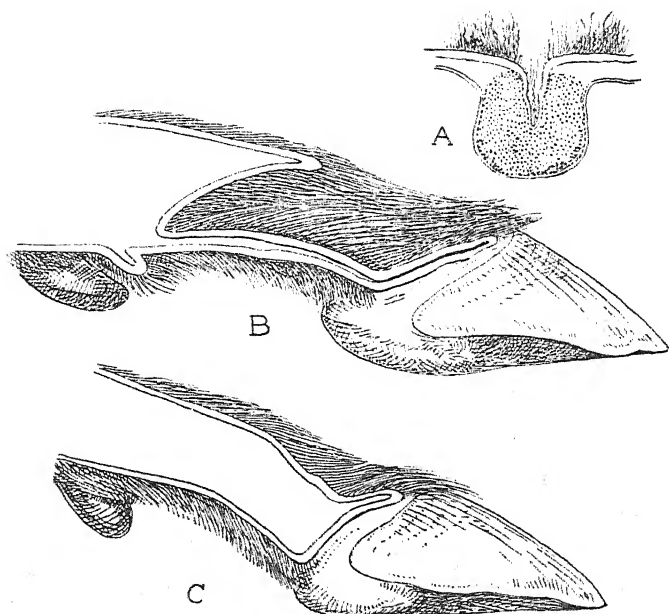
I am indebted to Mr. E. Gerrard for a mask, containing entire preorbital glands, and front and hind feet of this species.

The preorbital glands were covered with hairs which in the individual examined had a thickened appearance, owing to the coating of brown earthy-looking secretion which covered them individually. The centre of the area was marked by a distinct orifice leading into a narrow duct about half an inch long and lined with short hair. This duct penetrated about halfway into the large gland which was about as large as a walnut.

Pedal glands were present only on the fore feet, or if present on the hind feet they attained only a comparatively slight degree of development. On the fore feet they very closely resembled those of Gazelles, consisting of a very large interdigital cavity opening by a long orifice on the anterior aspect of the pastern and extending upwards from the proximal margin of the hoof in front. As in Gazelles the two hoofs were united by a deep interungual web, which extended from the heels to the proximal margin of the hoof in front, then folded sharply over and was continued backwards along its course nearly as far up as the false hoofs, where it turned obliquely forwards and downwards, meeting the skin of the front of the pastern at an acute angle to

form the anterior web joining the two halves of the pastern together in front. Although essentially of the same nature as in Gazelles this gland differed in one or two points. For instance, the height or length of the cavity along the back of the pastern was considerably greater than the length of the orifice, owing to the cavity being continued farther up the pastern than the edge of the anterior upper web. In the second place, the walls of the cavity were clothed with long blackish hairs which projected from the orifice, forming only a small tuft over the proximal margin

Text-fig. 106.

*Bubalis caama.*

- A. Vertical median section of preorbital gland.
- B. The same of front foot.
- C. The same of hind foot.

of the hoof. Lastly, the interungual web was quite naked back to the heels, and instead of meeting the skin of the back of the pastern at right angles met it at an obtuse angle, the difference of inclination being obviously correlated with the less upright position of the foot when standing, the long hoofs of the Hartebeest being much less vertical than the short hoofs of the Gazelles.

In the hind foot there was only a shallow depression just above

the hoofs, the skin of the interungual web being folded back for only a short distance, then inclining obliquely upwards, forming the back wall of the depression in question. This depression on the hind foot might be compared to the depression on the pastern of the Chamois, except that its walls were hairy instead of nearly smooth.

Of the genus *Bubalis* I have also examined the face-skin and part of the gland of *B. cokei* supplied to me by Rowland Ward, Ltd., and by Mr. E. Gerrard. In this species the pre-orbital gland has essentially the same structure as in *B. caama*.

The following species also have the gland clothed externally with a mat or tuft of hairs, namely, *B. major*, *tora*, *swaynei*, *leleuel*, and *jacksoni*. In *B. lichtensteini*, on the contrary, the glandular area is naked as in *Damaliscus*, the orifice in the dry skin being a small slit-like aperture leading into a duct. The hind foot of *B. lichtensteini* is like that of *B. caama*, having only a shallow depression on the front of the pastern. For the material of the species, enabling me to establish these data, I am indebted to Mr. E. Gerrard.

#### Genus DAMALISCUS Sci. & Thos.

DAMALISCUS KORRIGUM Ogilby. Subsp. JIMELA Matsch.

(Text-fig. 107.)

I am indebted to Mr. E. Gerrard for the opportunity of examining a complete skin of this Hartebeest.

The preorbital gland itself was cut away, but the orifice was represented by a short elongated aperture in the middle of a bare patch of skin in front of the eye.

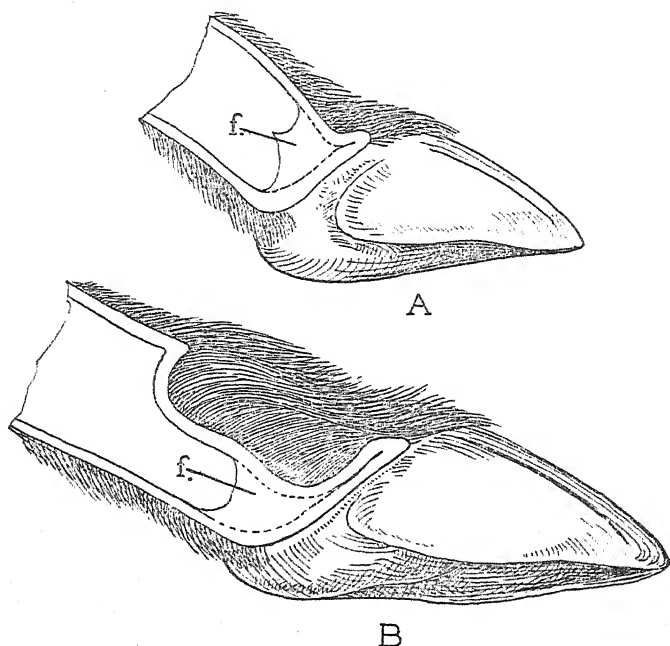
The pedal glands, present only on the front feet, resembled those of *Bubalis caama* in a general way, with the exception that the interdigital pit was much less deep, owing to there being a considerable space between the integument of the back of the pastern and that forming the posterior wall of the cleft; moreover, the skin of the front of the pastern, forming the upper edge of the orifice, was not folded backwards and upwards upon itself, but descended almost at right angles to form the short upper wall of the interdigital cleft. A further difference was seen in the presence of a vertical fascia joining the skin of the back of the pastern to that of the interdigital cleft just above the heels. The walls of the cleft were clothed with long rusty-red hairs, the ends of which projected from the orifice, overhanging the proximal end of the hoof in front.

The hind foot was like that of *B. caama*, except that the depression on the front of the pastern just above the hoof was shallower. A connecting fascia, corresponding to that of the hind foot, was also present.

The area of the preorbital gland on a face-skin of *D. korrigum tiang*, for which I am indebted to Rowland Ward, Ltd., resembled that of *D. k. jimela* in all respects.

The area in question is also bare in *D. hunteri*, *albifrons*, and *pygargus*. In an adult male of *D. albifrons* now living in the Gardens, the gland is usually active and tumid, secreting a substance which passes on to the face, staining the edges of the white blaze yellow. The orifice of the gland is circular and lies in the centre of the smooth glandular swelling. The gland itself, which I saw in a dead Blesbok many years ago, was, I clearly recollect, about as large as a filbert nut, with a short duct leading

Text-fig. 107.

*Damaliscus korrigum jimela.*

A. Median vertical section of hind foot.

B. The same of front foot.

f., fascia.

into it, exactly as in *B. caama*. In two young Bonteboks now living in the Gardens, the gland is much less prominent than in the Blesbok, possibly because the specimens are not yet adult.

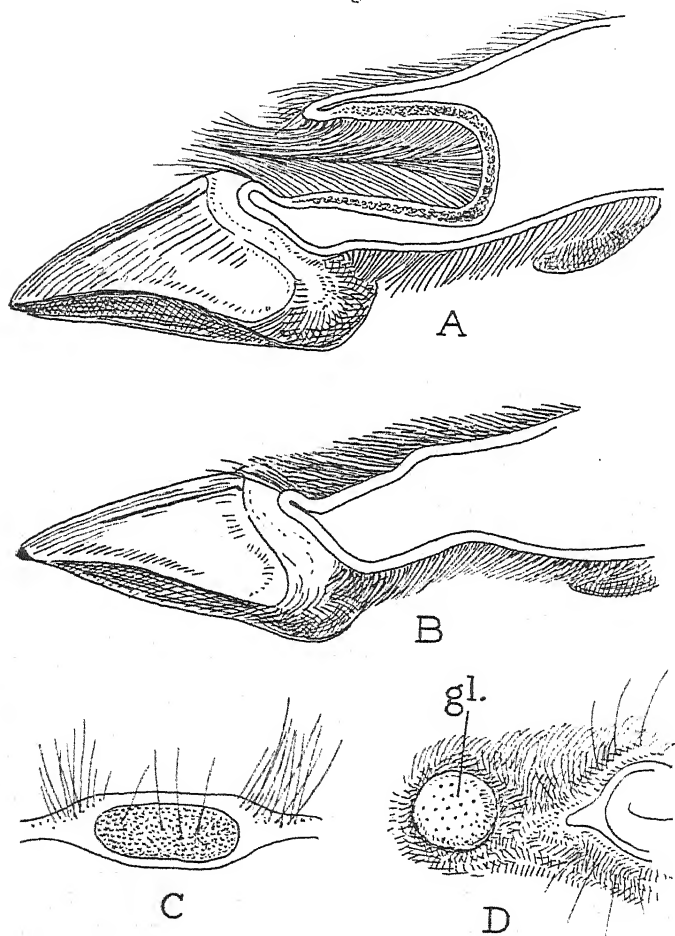
The above-described specimen of *D. korrigum jimela* had no inguinal glands; but the hair on the skin a short distance away from the one teat on each side was arranged in a whorl.

Genus *CONNOCÆTES* Licht.

*CONNOCÆTES* GNU Zimm. (The White-tailed Gnu.)  
(Text-fig. 108.)

Of this species I have examined two specimens, an immature male and an adult female. In both there were no inguinal glands and a single pair of teats.

Text-fig. 108.

*Connocætes gnu.*

- A. Median vertical section of front foot.
- B. The same of hind foot.
- C. Section of preorbital gland.
- D. Superficial view of preorbital gland (*gl.*).

The preorbital gland consisted of a subcircular patch of black skin, sparsely pitted with setal pores, whence hairs arose. In the young male the gland was as large as a hazel-nut, but markedly longer than deep. In section it was pink in colour and resembled a cyst enveloped in the thickened skin. It was not lodged in any depression of the skull, but merely rested on the bone of the face. The hairs which appeared upon its surface were seen to be rooted deep in the gland and to reach the surface through the pores above described. No secretion could be squeezed from the gland. This was perhaps due to the fact that the animal was immature and had been ailing for some time before death. It seems probable that the secretion naturally exudes through the setal pores. Nevertheless, I have never seen the preorbital gland of a living Gnu, either of this species or of *G. taurinus*, show any sign of secretion or even of moisture. I did not cut the gland of the adult female, since the specimen was required for preservation.

Pedal glands, as in *Bubalis*, are well developed only on the front feet and appear to be absent on the hind feet. The feet and the glands have essentially the same structure as in *Bubalis caama*. In the adult female, however, the cavity of the gland differed in some interesting particulars from that of *B. caama* above described. The posterior wall of the cavity was not folded so closely upon the skin of the interungual web and of the back of the pastern, but ran obliquely upwards and backwards, then turned forwards at a right angle, then downwards and forwards at a right angle closely in contact with the skin of the front of the pastern, which it joined at the upper end of the orifice at a very acute angle, forming a close fold. The anterior upper web thus constituted extended nearly as far downwards as the edge of the interungual web, leaving a much shorter orifice for the gland than in *Bubalis caama*. In the latter the gland was rhomboidal in section, whereas in *C. gnu* it was suboblong. It was thickly clothed with long hairs, projecting like a fringe or tuft from the orifice. The roots of all the hairs were covered and stuck together with blackish secretion smelling exactly like sour milk or cream-cheese. In the young male the cavity of the gland was nearly intermediate in shape between that of the adult and that of *B. caama*, the slit-like orifice being much longer than in the adult owing to the absence of the anterior wall, the anterior web or fold stopping short much higher up the pastern above the hoofs. In section the upper portion of the cavity resembled that of *B. caama*, while its lower portion was like that of the adult *C. gnu*.

On the hind feet there was only a very shallow hair-lined depression, recalling that of *Bubalis caama*.

The front and hind feet of another adult example, kindly given to me by Rowland Ward, exactly resembled the one above described.



## Genus GORGON Gray.

## GORGON TAURINUS Burch.

(The Brindled Gnu or Blue Wildebeest.)

Living examples of this species have the preorbital gland like that of *Connochætes gnu*; and in a dried skin, lent to me by Mr. E. Gerrard, I found the front and hind feet constructed exactly as in that species. One pair of teats only is visible in a pregnant female now living in the Gardens.

Gray long ago placed the White-tailed and the Brindled Gnus in distinct genera; and it was evidently the opinion of Messrs. Selater and Thomas that there was a great deal to be said in favour of this view, although they did not give it practical expression in their 'Book of Antelopes.' Judged by modern standards it appears to me that the well-known differences between the two are quite worthy of generic recognition. There can be no evasion of this conclusion if specific value be given, as is commonly done, to the differences between the Brindled and White-bearded Gnus. The White-tailed Gnu is a very differently built animal from the two just mentioned. The back is not sloped as in the rest of the Bubalinae, but horizontal, and the hind-quarters are markedly elevated on account of the prominence of the summits of the iliac bones. Other external features separating this species from the Brindled Gnu and from its ally, the White-bearded Gnu (*G. albo-jubatus*), are well known, and are in my opinion equivalent to those separating *Bubalis* and *Damaliscus*.

Using the preorbital glands as a basis, the genera of Bubalinae may be distinguished as follows:—

- a. Preorbital gland marked with a central orifice leading into a hair-lined tube, which dips into the substance of the gland.
- b. Surface of the preorbital gland naked or nearly so. *Damaliscus* and *Bubalis lichtensteini*.
- b'. Surface of the preorbital gland thickly and uniformly covered with long hair ..... *Bubalis*.
- a'. Preorbital gland without any central orifice and tube, its free surface consisting of an area of skin sparsely covered with hairs ..... *Connochætes* and *Gorgon*.

Since Lichtenstein's Hartebeest, hitherto referred to the genus *Bubalis*, is known to depart from the other species of that genus in the structure of its horns and also in the nakedness of the preorbital gland, it should perhaps be referred to a distinct genus. In diagnosing the genera in this table, no use has been made of the differences recorded in the structure of the pedal glands of *Connochætes gnu*, *Bubalis caama*, and *Damaliscus korrigum*, striking though they be, because they have only been noted in a single species of each of the genera.

The structure of the feet and the presence of pedal glands only on those of the anterior pair bear out the evidence from other sources that the Gnus and Hartebeests form a natural

group. Moreover, it seems to me that the size and structure of the preorbital gland and of the glands in the front feet, coupled with the hairiness of the rhinarium and the presence of a single pair of mammae, suggest tolerably close kinship between *Damaliscus*, the least-specialised member of the Bubalinae, and the Antilopinae. At all events, I think it may be claimed with some assurance that the relationship indicated is closer than that between *Epyceros* and the Antilopinae.

#### Subfamily ORYGINÆ.

I prefer to use the term Oryginae for the group called Hippotraginae by most modern authors, because the generic name *Hippotragus* will soon, probably, no longer be admitted as a valid generic designation, being antedated both by *Oxanna* and *Egoceros*.

#### Genus ORYX Blainv.

According to Owen the following species of this genus have neither preorbital nor inguinal glands: *O. gazella* (= *A. oryx*) and *O. algazel* (= *A. leucoryx*).

Ogilby also says that these two species have neither preorbital nor inguinal glands, but states that the pedal glands are large and that there are two pairs of mammae.

#### ORYX BEISA Rüpp. (The Beisa.)

(Text-fig. 109, C.)

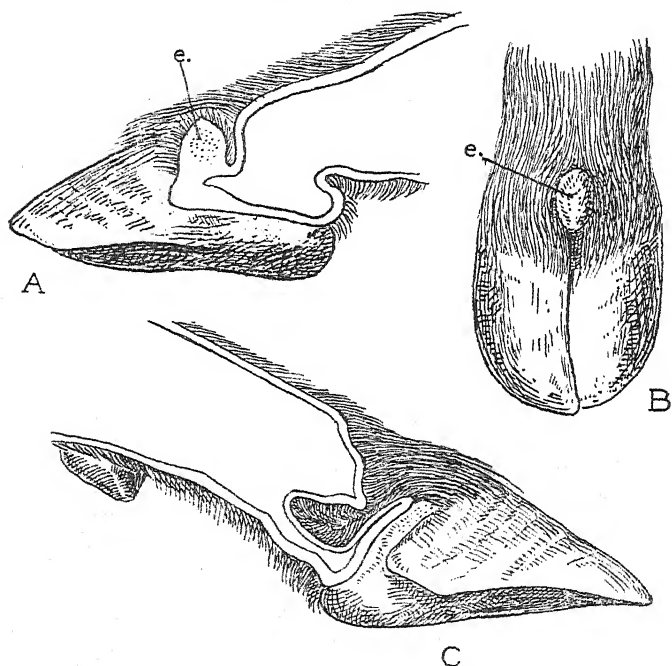
In the dried skin of a young male example of this species, for which I am indebted to Mr. Gerrard, I could find no trace of preorbital glands nor of inguinal glands, but two pairs of mammae were present.

Pedal glands, approximately similar in structure, were present on all four feet. They opened by an elongated, somewhat lanceolate interdigital cleft on the front of the pastern just above the hoofs. This cleft led into a shallow depression, which at its deepest part, close to the interungual web, passed into the principal part of the gland, which consisted of a moderate-sized sac extending for a short distance upwards and backwards almost as far as the posterior integument of the pastern. Describing the gland another way, it might be said to consist of a deep but rather short interdigital depression subdivided into an anterior and posterior part by a ridge of integument projecting from its upper wall, thus constricting its lumen.

The floor and posterior wall of this depression were formed by the closely infolded layer of the interungual web. Its opposite walls were formed by the integument of the front of the pastern, which sloped obliquely downwards and forwards to the aforesaid ridge, then obliquely upwards and backwards. The entire interdigital depression on both sides of the constriction was clothed with longish white hairs clogged with secretion. Inferiorly, just below the orifice, the hairs were longer and overlapped the

proximal edge of the nail of the hoof. The interungual web was thick and horny and, as in the Antilopinae and Bubalinae, extended from the heels to a point near the anterior margin of the hoof before being closely folded upon itself; and, as in the Bubalinae, *Antilope*, *Hippotragus*, and the Tragelaphinae, it was quite smooth.

Text-fig. 109.



- A. Median vertical section of front foot of *Addax naso-maculatus*: e., conical excrescence with the depression behind it.  
 B. Anterior view of the same foot: e., conical excrescence.  
 C. Median vertical section of hind foot of *Oryx beisa*.

The hoofs were pointed, compressed above, with broad flat heels and flat soles. The only difference noted between the glands of the front and hind feet was the greater development of the constricting ridge in those of the hind feet.

The interdigital glands of *Oryx beisa* with their longer cleft-like orifice occupy a nearly intermediate position between those of Gazelles and those of *Hippotragus*.

#### ORYX LEUCORYX Pall.

(The White Oryx = *O. beatrix* of most authors.)

In an old dried skin of a male example from the shores of the

Persian Gulf, kindly lent to me by Mr. Gerrard, the pedal glands, though imperfect, had apparently the same structure as in *O. beisa* and there was no trace of inguinal glands.

#### ORYX ALGAZEL Oken.

(The Soudanese Oryx = *O. leucoryx* of most authors.)

Both Owen and Ogilby state that this species has no pre-orbital gland. I presume this observation was based upon an examination of dried skins or of skulls. It is not, however, true; for in the example now living in the Gardens there is quite commonly a small patch of secretion sticking the hairs together about an inch in front of the eye. This proves the existence of a specialised glandular area beneath the hairs; but probably the gland is not highly developed.

#### Genus HIPPOTRAGUS Sund.

According to Owen, the following species of this genus have neither preorbital nor inguinal glands: *H. leucophaea*, *equina* (= *barbata*).

The only species of this genus examined by Ogilby was *H. leucophaea*, which he referred to the genus *Oryx*. He agreed with Owen that this species has neither inguinal nor preorbital glands, but adds that the pedal glands are large and that there are two pairs of mammae. W. L. Selater also states that in the genus *Hippotragus* the preorbital gland is absent and that there are two pairs of mammae.

#### HIPPOTRAGUS NIGER Harris. (The Sable Antelope.)

(Text-fig. 110.)

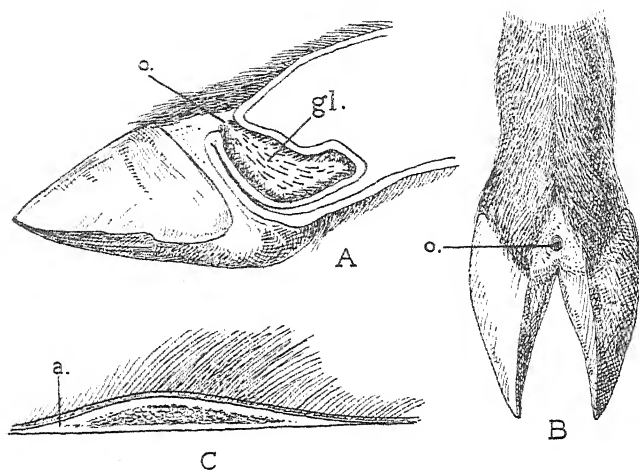
In an adult female of this species which died in the Gardens I found a preorbital gland underlying the white preorbital tuft of hair. It was very little differentiated, however, consisting, like the knee glands of Gazelles and some Sheep, of thickened vascular integument. The bases of the white hairs were crowded with pale yellow grains like scurf, smelling of a mixture of sour milk and new-mown hay.

There were no inguinal glands.

The pedal glands were well developed on all four feet and opened to the exterior by a small subcircular orifice in the centre of a naked patch of skin in a shallow depression close to the proximal end of the hoofs. The gland was a large sac passing obliquely upwards and backwards and reaching as far as the posterior integument of the pastern, and with its lower wall closely applied inferiorly to the interungual web which was sharply folded back upon itself, the infolded portion constituting the wall of the gland in question. The walls of the gland were covered with short hairs, becoming longer towards the orifice of the gland.

The interungual web of the hoof was smooth from the orifice of the gland to the posterior area of the heels.

Text-fig. 110.

*Hippotragus niger.*

A. Median vertical section of front foot: *gl.*, pedal gland; *o.*, its orifice.

B. Anterior view of front foot: *o.*, orifice of gland.

C. Longitudinal section of preorbital gland; *a.*, ocular end of gland.

I was able to verify these facts upon a second specimen, a dry skin kindly lent to me by Mr. Gerrard. This specimen had two pairs of teats, but no trace of inguinal glands was discoverable.

#### HIPOTRAGUS EQUINUS Is. Geoff.

(The Roan Antelope.)

In a female specimen with two pairs of teats, but no inguinal glands, for the examination of which I am indebted to Mr. Gerrard, I found the pedal glands to be of substantially the same structure as in *H. niger*, except that there was a slight constriction of the lumen of the gland, caused by a small integumental ridge rising from its upper wall and partly dividing it into an outer and an inner chamber, as in *Oryx beisa*.

#### Genus ADDAX Raf.

ADDAX NASO-MACULATUS Licht. (The Addax.)

(Text-fig. 109, A, B, p. 908.)

According to Owen, this species has neither preorbital nor inguinal glands.

I have seen only the front and hind feet of one dead example, no other material being available.

The feet were very different from those of *Oryx* and *Hippotragus*, being low, flat, long-heeled, and broad at the point in adaptation to a soil of soft sand. In section, the integument of the posterior surface of the pastern was seen to be folded just above the heels like that of *Pantholops*. From that point it passed forwards for some distance parallel with the sole of the foot before turning abruptly upwards towards the front of the pastern. Here it passed into a somewhat conical excrescence or eminence, covered with short hair and defined behind and laterally by a semicircular infolding or depression of the skin. Behind this excrescence, the integument of the anterior surface of the pastern was continued straight up this area without sign of insinking and was covered with normal longish hairs. The latter inferiorly encircled the excrescence, which jutted up like an island from their midst. I believe the excrescence to be glandular. The structure of the two feet was the same, except that the excrescence was smaller on the foot which I judged to belong to the hind leg.

Examination of the feet of a very young example now living in the Gardens revealed no signs of the excrescence, but there was a distinct orifice, representing, I suppose, the infolding of the skin defining the excrescence in the adult. This orifice was in almost the same position as the orifice of the gland in *Oryx*, and its glandular nature was attested by the staining yellow of the white hairs round it.

*Addax* has a marked patch of longer hairs below the eye on each side of the face. This probably overlies a glandular thickening of the skin, such as is present in *Hippotragus*. I have, however, no direct evidence of the fact.

From the structure of the feet *Addax* would seem to be less closely allied to *Oryx* and *Hippotragus* than these two are to one another. But more and better material of the genus must be examined before any satisfactory conclusion as to its true systematic position can be arrived at.

#### Subfamily CERVICAPRINÆ.

##### Genus PELEA Gray.

##### PELEA CAPREOLUS Bechst. (The Vaal Rhebok.)

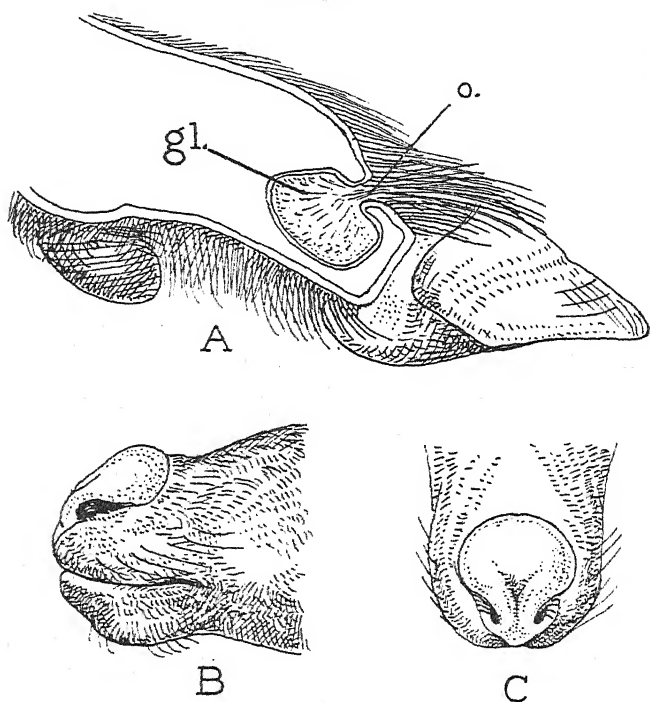
(Text-fig. 111.)

According to Owen, this species possesses inguinal glands, but has no preorbital glands.

The absence of preorbital glands has been affirmed by subsequent authors, and correctly so, judging from the one specimen of this species I have examined, a female brought by Dr. Lyster Jameson from S. Africa, which lived two years in the Gardens. This specimen, however, had no trace of inguinal glands. Pedal glands were well developed on all four feet. They opened by a

small circular orifice on the front of the foot in a shallow depression lined with long hairs. The orifice led into a short hair-lined duct which expanded into a capacious but laterally compressed thin-walled sac reaching almost to the posterior integument of the fetlock. The sac was filled with semifluid, pale-coloured, evil-smelling secretion, recalling exactly the odour of dog's dung. Close to the orifice in the depression arose a number of long hairs overhanging the base of the hoofs in front, and these were stuck together with the secretion, which could be easily squeezed from the gland by pressure applied to the sides of the pastern.

Text-fig. 111.

*Pelea capreolus* ♀.

A. Median vertical section of hind foot: *gl.*, pedal gland; *o.*, its orifice.  
B & C. Lateral and dorsal views of the nose to show swollen rhinarium.

The structure of the feet was almost the same as in *Cervicapra redunca*, the interungual integument being quite naked, meeting that of the back of the pastern at a right angle and forming an obtuse angle with the floor of the depression on the front of the fetlock. Thus the integument or "web" joining the hoofs

together extended from the heels almost up to the proximal end of the anterior ridge of the nail. The apical angle of the nail was also less acute than in *Cervicapra redunca* and *Adenota kob*, the hoofs more approaching those of Goats and Sheep in shape—in accordance, no doubt, with the mountain habitat of *Pelea*.

A well-known distinguishing feature of *Pelea* as compared with *Cervicapra* and *Kobus* is the enlarged and swollen rhinarium, which has a widely rounded posterior border extending backwards beyond the posterior notch of the nostril. This rhinarium is glandular. In the living animal it became studded with drops of moisture under the stimulus of excitement or pleasure, and after death was easily made by pressure to yield the same substance.

Like *Cervicapra* and *Kobus*, *Pelea* has two pairs of mammae.

#### Genus CERVICAPRA Blainv.

Owen noticed the absence of preorbital and the presence of inguinal glands in three species of this genus, namely, in *C. redunca*, the Nagor, a Senegambian species; in *C. arundinum*, which he quoted as *Antilope eleotragus*; and in *C. fulvorufula*, if I am right in supposing he meant this species by *A. landiana*, the latter name being, I surmise, written in error for *lalandia* or *lalandii*.

I have examined only fresh material of one species, namely the following.

#### CERVICAPRA REDUNCA Pall. (The Nagor.)

(Text-fig. 112.)

Owen does not state how many inguinal glands he discovered in the species he examined, but in two examples of *C. redunca*, from Senegambia, presented by Sir George Denton, I found two pairs of sacs. The anterior sac on each side was wide-mouthed but shallow, the glandular area into which it dipped being only slightly vascular. The posterior sac, lying rather nearer the middle line and close to the scrotum, was, on the contrary,  $1\frac{1}{2}$  inches deep, of even width throughout, the orifice being about  $\frac{1}{2}$  an inch in diameter and not half the width of the orifice of the anterior sac. Its glandular area was very thick and vascular. Both pouches secreted a semifluid substance, turning yellow and waxy at the orifice and giving off an odour of flour-paste going stale, which to me was most nauseous.

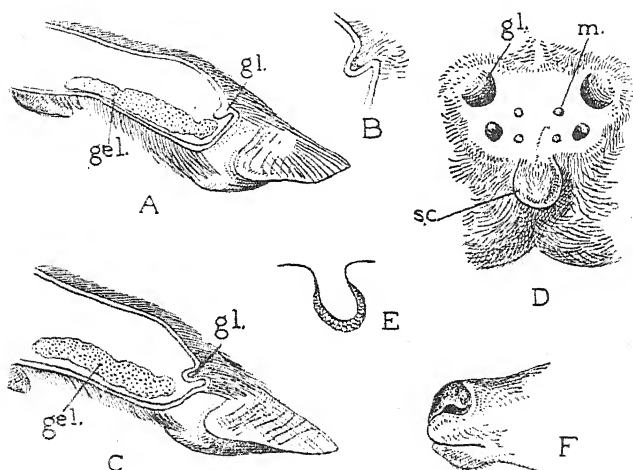
There were no preorbital glands.

In one specimen I found no trace of pedal glands; but in the other there was a very small hair-lined pouch opening into the shallow hair-lined depression on the front of the pastern just above the angle formed by the junction of the integument of this surface with the strip of naked skin extending from the front to the heel of the hoofs and binding the two together. There



appeared to be no gland connected with this pocket, since there was no secretion on the hairs projecting from its orifice; but beneath the pocket between the phalanges there was an elongated mass of vascular gelatinous tissue extending almost as far up as the false hoofs, just such as is found in the hoofs of Oxen. The fore and hind feet were alike, except that the anterior depression was somewhat deeper on the hind feet, allowing a slightly wider spread to the hoofs, and whereas the false hoofs were united by thick horny material on the fore feet, those of the hind feet were connected by naked skin.

Text-fig. 112.

*Cervicapra redunca.*

- A. Median vertical section of front foot taken a little to one side of the aborted gland (*gl.*): *gel.*, gelatinous interdigital mass.
- B. The aborted gland of the same in section.
- C. Median vertical section of hind foot: lettering as in A.
- D. Inguinal region showing four mammary (*m.*); scrotum (*sc.*) and inguinal glands, the anterior pair (*gl.*) wide and shallow, the posterior pair behind them narrow and deep.
- E. Section of inguinal gland of posterior pair.
- F. Side view of nose to show rhinarium.

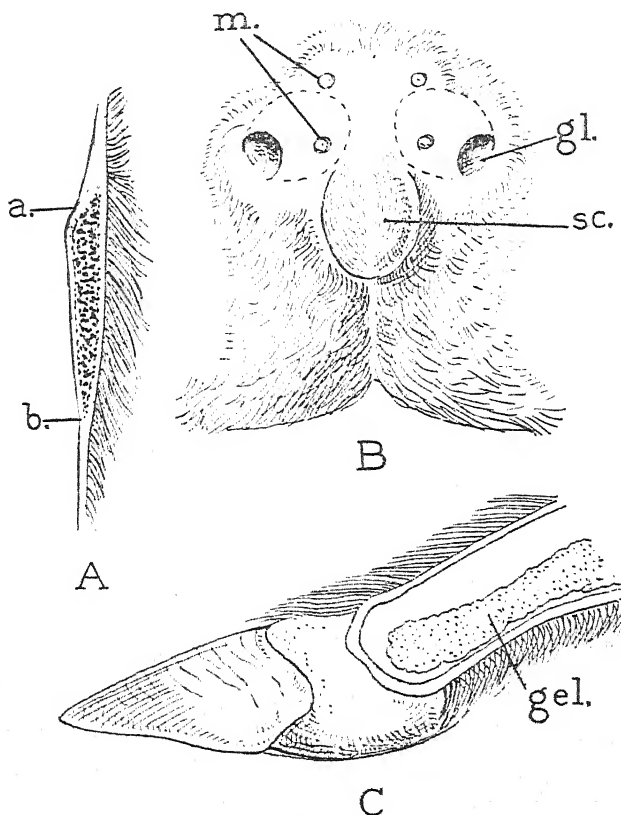
In both specimens there were two pairs of mammary; but in neither was there a bare patch of skin below the ear. The knees had a bare patch of thickened horny skin, which was apparently, however, not glandular. So far as the pedal glands are concerned, the genus *Cervicapra*, as represented by *redunca*, stands in the same relation to *Pelea capreolus* as *Capra* stands to *Ovis*; and there cannot, I think, be much doubt that the ancestors of existing species of *Cervicapra* are descended from Antelopes with pedal glands like those of *Pelea*.

Genus *ADENOTA* Gray.*ADENOTA KOB* Erxl. (Buffon's Cob.)

(Text-fig. 113.)

According to Owen, this species has inguinal pits but no preorbital glands.

Text-fig. 113.

*Adenota kob.*

- A. Longitudinal section of preorbital gland: *a.*, upper or ocular end; *b.*, lower end.  
 B. Inguinal region: *m.*, mammae; *sc.*, serotum; *gl.*, orifice of gland, the subcutaneous extension of which is shown by the dotted line.  
 C. Median vertical section of front foot; *gel.*, gelatinous interdigital mass.

I have seen two examples of this species, a subadult male from Upper Nigeria presented by Lady Constance Stewart Richardson,

and an immature female from Sierra Leone presented by Mr. Tuling.

In the female there was a distinct preorbital gland, marked externally by a tuft of hair darker in colour and a little longer than that of the surrounding area. Beneath this the skin was considerably thickened, the thickest part being situated above towards the anterior angle of the eye and the thinnest part below, where the thickening gradually merged with the normal skin of the cheek. In its essential characters this gland resembled that of the Sable Antelope above described (p. 910). The male was not examined for this character.

Both specimens had two pairs of teats and a single pair of inguinal glands representing the posterior pair found in *Cervicapra redunca*; but in addition to these there was upon the right side in the female a very minute pocket lying far out and in advance of the mammae. There was no trace of this on the left side. The orifice of the large gland was subcircular, about  $\frac{1}{2}$  an inch in diameter in the male and  $\frac{1}{4}$  of an inch in the female; the pouch itself was capacious, widening considerably within the orifice and extending for 1 inch in the female and  $1\frac{1}{2}$  inches in the male in the direction of the scrotum and mammae. The yellow secretion had exactly the same nauseating smell as that of *Cervicapra redunca*, namely of flour-paste or starch. There were no pedal glands and no trace even of the duct. The structure of the feet was the same as in *Cervicapra redunca*, with the same elongated mass of vascular gelatinous tissue lying between the penultimate phalanges along the inner surface of the skin of the back of the pastern. The skin round the false hoofs was naked.

#### Genus KOBUS Smith.

KOBUS ELLIPSIPRYMNUS Ogilby, DEFASSA Rüpp., and MARLE Gray.  
(Water Bucks.)

According to Owen, *K. ellipsiprymnus* has neither preorbital nor inguinal glands.

It is on account of the alleged absence of the inguinal glands in this species and their presence in *A. kob* that I keep the two species under separate generic headings. Trouessart regards them as representing distinct subgenera, presumably for other reasons.

On the skin of the head of an example of *K. defassa*, from the White Nile, lent to me by Rowland Ward, Ltd., I could find no trace of a preorbital gland; but I think a gland resembling that of *Adenota kob* will probably be found when fresh material is examined. The fore and hind feet of *K. marie* (Mrs. Gray's Water Buck), given to me by Mr. Gerard, showed no trace of pedal glands, the feet in section resembling those of *A. kob*.

The genera of this subfamily, so far as my observations extend,

may be distinguished as follows, using the glands as a basis for their separation :—

- a. Pedal glands present on all four feet and opening by a short duct with a small circular orifice on the front of the pastern just above the hoofs; summit of rhinarium swollen and glandular, and extending back beyond the posterior edge of the nostrils; no inguinal glands ..... *Pelea*.
- a'. Pedal glands represented at most by the duct of the glands present in *Pelea*; summit of rhinarium normal, not extending behind the posterior notch of the nostrils.
  - b. With two pairs of inguinal glands; tail bushy as in *Pelea*... *Cervicapra*.
  - b'. Inguinal glands absent or represented by a single pair of pouches; tail tufted at the end.
  - c. A single pair of inguinal glands ..... *Adenota*.
  - c'. No inguinal glands ..... *Kobus*.

In their volume on the Mammalia, Flower and Lydekker classified the genera above referred to the Cervicaprinæ with the Neotraginæ. The Cervicaprinæ, however, differ markedly from the Neotraginæ, so far as my observations extend, in the structure of the feet, since they entirely lack the deep and long interdigital cleft on the front of the pastern found in the Neotraginæ.

It seems to me that, in looking for the relationships of the Cervicaprinæ on the lines followed in this paper, the following facts should not be ignored. With the exception of the Indian genera of Tragelaphinæ, the preorbital gland is absent in that group; and in the Cervicaprinæ it is at most represented by an integumental thickening. In both groups, and in no other subfamilies of Bovidæ, two pairs of inguinal pouches have been recorded. More significant still is the fact that the structure of the feet, whether pedal glands be present or absent, is the same in the Cervicaprinæ as in the Tragelaphinæ. Corroborating these characters are the presence of two pairs of mammæ and a moderate or large rhinarium, to which may be added the invariable absence of horns in the females of Cervicaprinæ and in most genera of Tragelaphinæ. I do not, however, attach much importance to this character, despite the value given to it by some writers\*.

At all events, it must, I think, be conceded that the Cervicaprinæ are more akin to the Tragelaphinæ than they are to the Antilopinæ, Bubalinæ, Neotraginæ, Cephalophinæ, or Oryginæ, although the retention by *Pelea* of pedal glands, somewhat recalling those of the Oryginæ, is a fact full of interest.

The following genus is possibly related to the Cervicaprinæ (see p. 897).

#### Genus AMMODORCAS Thos.

#### AMMODORCAS CLARKEI Thos.

(The Dibatag or Clarke's Gazelle.)

The only materials of this genus and species I have seen are

\* W. L. Slater, for instance, who uses it as a basis for grouping the S. African subfamilies of Bovidæ.

some dried skins in the British Museum. I made, however, no dissections. Superficially the feet showed no trace of pedal glands. Certainly there were none such as exist in the Antilopinae; and I judged that the feet resembled those of *Epyceros* or *Kobus*. Also there were two pairs of well-developed teats, and I could find no evidence of the existence of inguinal glands. These features, coupled with the long "bovine" tail and the shape and direction of the horns, which are more Cervicaprine than Gazelline, should exclude the genus from the Antilopinae. On the other hand, the preorbital glands appear to be like those of *Gazella*, and the muzzle is hairy as in that genus. The skull also is very Gazelline.

These cross-resemblances make *Ammodorcas* extremely difficult to classify. It has been described as intermediate between *Gazella* and *Lithocranius*. This is true of the length of the neck, the structure of the upper lip, and some characters connected with the skull. On the other hand, in the structure of the feet, horns, and tail, the genus is less Gazelline than *Lithocranius*: and I am disposed to think that the degree of relationship to *Gazella* that the two exhibit may be fairly gauged by the fact that the type-species of *Lithocranius* was referred to *Gazella* by so high an authority as Sir Victor Brooke, and was for a long time cited under that genus; while the type-species of *Ammodorcas* was originally assigned on equally good authority to the genus *Cervicapra*. From this it may be inferred that the kinship between *Lithocranius* and *Gazella* is tolerably obvious and that between *Ammodorcas* and *Gazella* by no means evident.

### Subfamily ÆPYCERINÆ.

#### Genus ÆPYCEROS Sund.

ÆPYCEROS MELAMPUS Licht. (The Impala or Pallah.)

(Text-figs. 114, 115.)

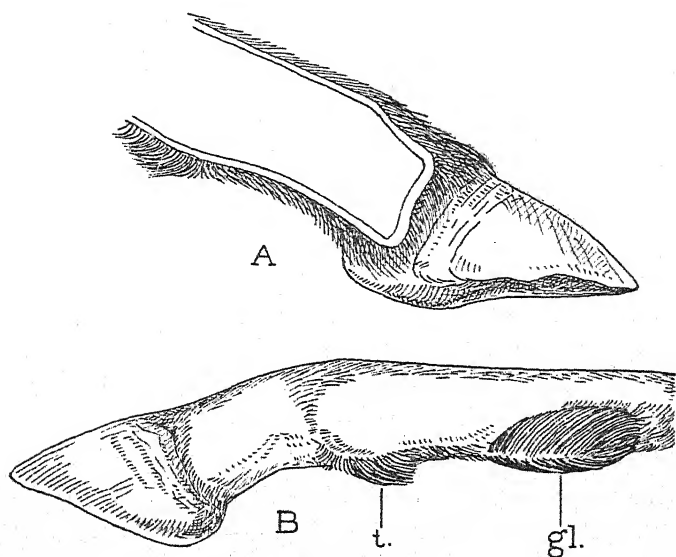
According to Owen, this species has large preorbital glands and inguinal glands as well. All recent authors, however, are in agreement that there are no preorbital glands, and I could find no trace of them on any of the dried skins in the collection of the British Museum.

I am indebted to Messrs. Rowland Ward, Ltd., and to Mr. E. Gerrard for the opportunity of examining and cutting open the hind feet of two specimens, and of thus being able to establish the absence of pedal glands on these limbs; and, so far as I can judge from looking at the fore feet of skins in the British Museum, they are equally absent in the front legs, the feet of which seem to be constructed exactly like those of the posterior pair except for the absence of the two metatarsal glands, well known and often recorded as present on each hind leg.

Of these glands W. L. Selater says: "attached to the lower ends of the cannon-bones of the hind legs is a brush of very dark brown

hairs surrounding the opening of a peculiar gland containing a fatty secretion." This is not quite an accurate description of the glands, according to my observations. The long blackish hairs marking each gland form a subelliptical elongated mat. The hairs point downwards, but those on each side of the middle line of the mat are inclined inwards, meeting at their tips and marking a central streak. When these converging hairs are pulled on one side it may be seen that they overlap an elongated area of naked skin, broadest across the middle, pointed above and below, and more than twice as long as wide. This naked area was covered, in the specimen examined, with secretion and the skin composing

Text-fig. 114.

*Epyceros melampus.*

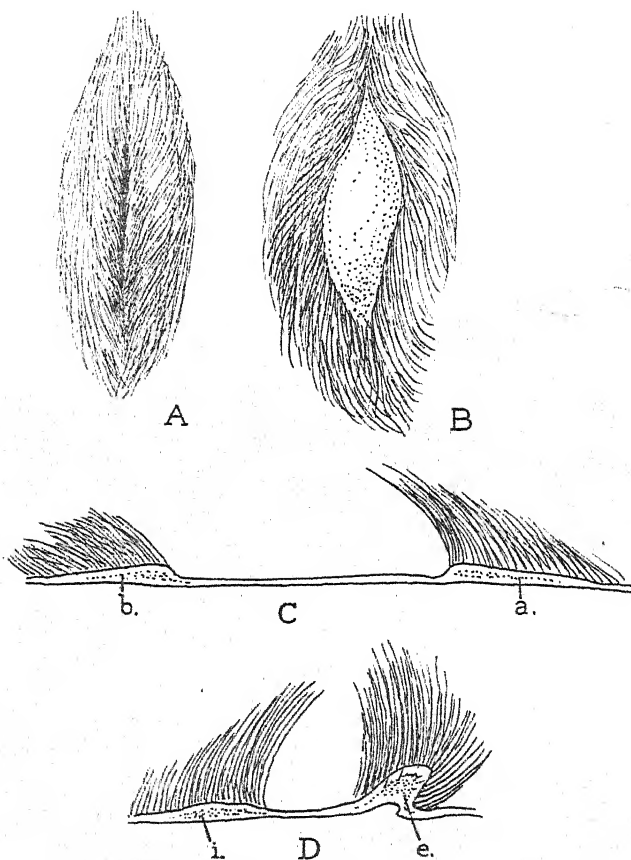
- A. Median vertical section of hind foot.  
 B. Hind foot to show the mat of hairs (*gl.*) marking one of the metatarsal glands and the tuft (*t.*) representing the false hoofs.

it was shown in section to be exceedingly thin. The skin surrounding it was, however, markedly thickened, especially externally, where it formed a distinct upstanding ridge. It was upon this thickened skin that the long hairs forming the mat grew; and, since the bases of these hairs were clogged with secretion, I infer that the thickened rim of skin is the secreting area of the gland and that the depressed naked area constitutes the floor of a kind of reservoir for the secretion, which is conducted downwards by the downward-growing long hairs.

The area of the false hoofs, which are themselves absent, is

covered with a thick mat of longish mostly black hairs directed backwards and upwards. The skin beneath this mat was thick and horny, but I could not find any evidence either upon the hairs or in the skin of special glandular development.

Text-fig. 115.

*Æpyceros melampus.*

- A. One of the metatarsal glands with the hairs undisturbed.
- B. The same with the hairs pulled aside to show the area of naked skin beneath.
- C. Longitudinal section of the gland: *a*, its upper, *b*, its lower end.
- D. Transverse section of the same: *e*, its external, *i*, its internal edge.

The feet themselves were constructed as in the Tragelaphinæ and most Cervicaprinæ, except that the whole interungual integument, forming the web, was covered with short hairs from front to back.

Although Gray long ago made the genus *Epyceros* the type of a special family, it has of late years found a place amongst the Antilopinae. Apart, however, from the hairiness of the rhinarium and of the interungual integument of the feet, it has very few "Antilopine" features, in the strict sense of the word. This latter feature, moreover, is as much Neotragine as Antilopine. In other respects, the feet may be described as Tragelaphine or Cervicaprine, except for the disappearance of the false hoofs and the presence of the metatarsal glandular mats of hair. The horns moreover, are as much Cervicaprine as Antilopine in character, and the absence of the preorbital gland is another feature excluding the genus from the Antilopinae.

Hence, taking into consideration the sum total of its characters, the peculiarities of *Epyceros* seem to me to be best expressed by setting it in a subfamily apart from all others.

#### Subfamily TRAGELAPHINÆ.

##### Genus TETRACEROS Leach.

##### TETRACEROS QUADRICORNIS Blainv.

##### (The Four-horned Antelope.)

(Text-figs. 116, A, B; 117, 118, 119, A, B, C.)

Hodgson described the preorbital glands of the genus *Tetraceros* as linear and longitudinal, and stated that inguinal glands are absent and pedal glands absent or present only on the hind feet. Blanford repeated this account with the additional information that the pedal glands are confined to the hind feet.

I have seen three examples of this species, a still-born young one and an adult male and female. In all the preorbital gland was well developed and valvular, consisting of a longitudinal pocket, the upper rim of which was produced into a large overlapping flap, forming a longitudinal slit where its free margin came into contact with the skin below it. When the flap was lifted a blackish nearly naked area was exposed; the posterior or ocular end of this area was the deepest portion of the invagination, which from that point forwards became gradually shallower. The gland itself was thick and pale in colour. In the adult male it was much larger than in the adult female, and in the summer discharged a quantity of soft cheesy-yellow secretion. The odour of this was not noted after death, the specimen having been preserved in alcohol; but in the fresh female specimen the drops of clear fluid that were squeezed from the gland had a faint aromatic scent.

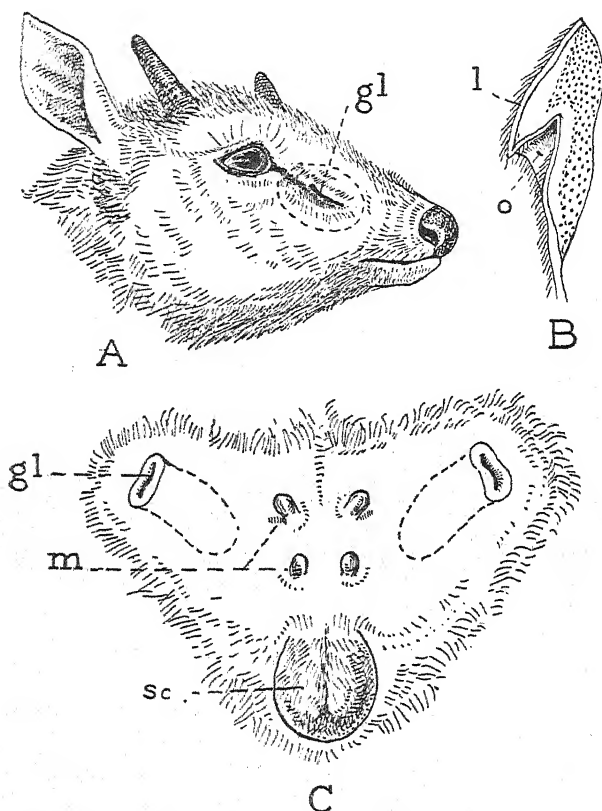
There were two pairs of teats, but no trace of inguinal glands.

The feet were constructed as in the genus *Tragelaphus*, the hoofs being short and but little distensible, owing to the extension of the interungual integument from the heels forwards for some distance before curving backwards to join that of the front of the



pastern, merely a shallow depression being formed. There was no trace of any folding of the integument constituting an interdigital cleft or gland such as is seen in the *Cephalophinae*, *Antilopinae*, and *Neotraginae*. The interungual skin, moreover, was

Text-fig. 116.

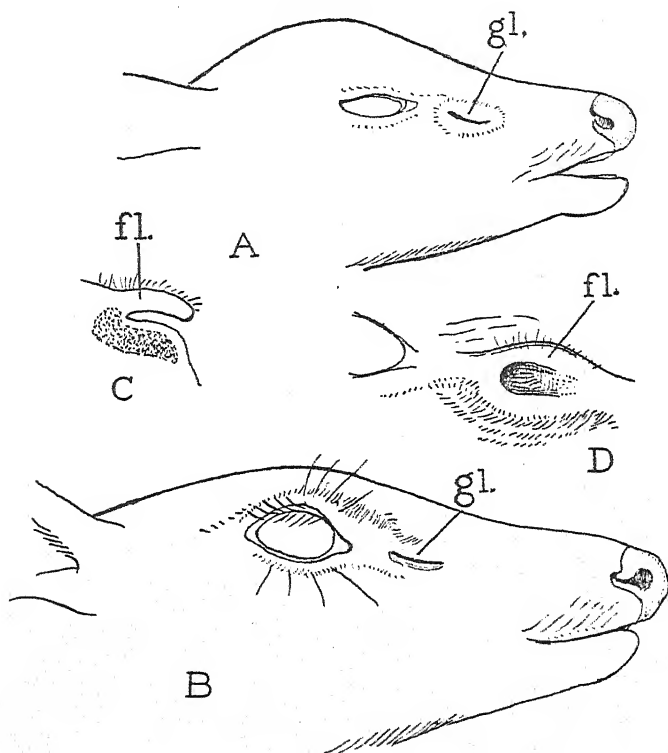


- A. Head of *Tetraceros quadricornis* ♂: orifice of gland (*gl.*); area of gland represented by dotted line.  
 B. Transverse section through the gland: *o*, its orifice; *l*, flap of skin constituting its upper lid.  
 C. Inguinal region of *Tragelaphus scriptus scriptus* ♂: *m.*, mammae; *sc.*, scrotum; *gl.*, orifice of gland; the subcutaneous extension of the gland shown by a dotted line.

naked. In the male there was a small accumulation of material on the hairs in the shallow depression of the front of the pastern just above the smooth area of the interungual integument; but there was no evidence that this was an odorous secretion. In the adult female, a much older animal, however, there was on all four

feet a large black horny excrescence occupying the same position and large enough to be visible without separation of the hoofs. The skin from which this excrescence arose was thrown into a multitude of columnar folds. Since I have seen no such excrescence on the feet of any other specimen of this Antelope, I must regard its development in this example as abnormal, perhaps pathological.

Text-fig. 117.

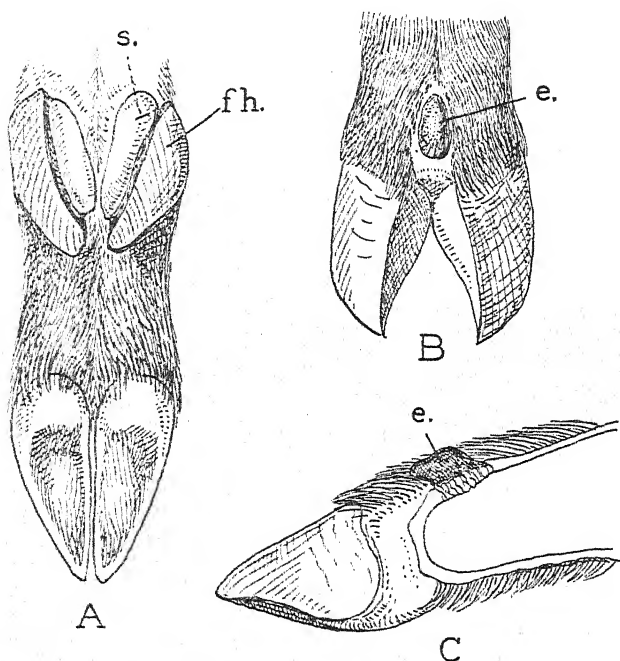
*Tetraceros quadricornis.*

- A. Head of newly born young: *gl.*, preorbital gland.
- B. Head of female: *gl.*, preorbital gland.
- C. Section of the preorbital gland of the same: *fl.*, flap of skin constituting its upper lid.
- D. Preorbital gland of the same with the lid (*fl.*) raised.

One of the most interesting features connected with this genus is the presence of a pair of well-developed glands between the false hoofs of the hind legs. In both the male and the female the false hoofs were large and the skin between them was black, tumid, horny, but soft and naked, except for a longish fringe along

the middle line. When squeezed a yellowish buttery substance with a strong sour odour exuded from a pair of smallish apertures, one on each side close to the middle line, so that the hairs became clogged with it. This aperture led into a voluminous sac, very scantily clothed with short pale hairs, the two sacs being separated by a narrow partition and occupying otherwise the whole area between the two false hoofs. Each was filled with the odorous substance above-mentioned, which, in the male at least, presented a concentrically stratified arrangement and was greenish in colour.

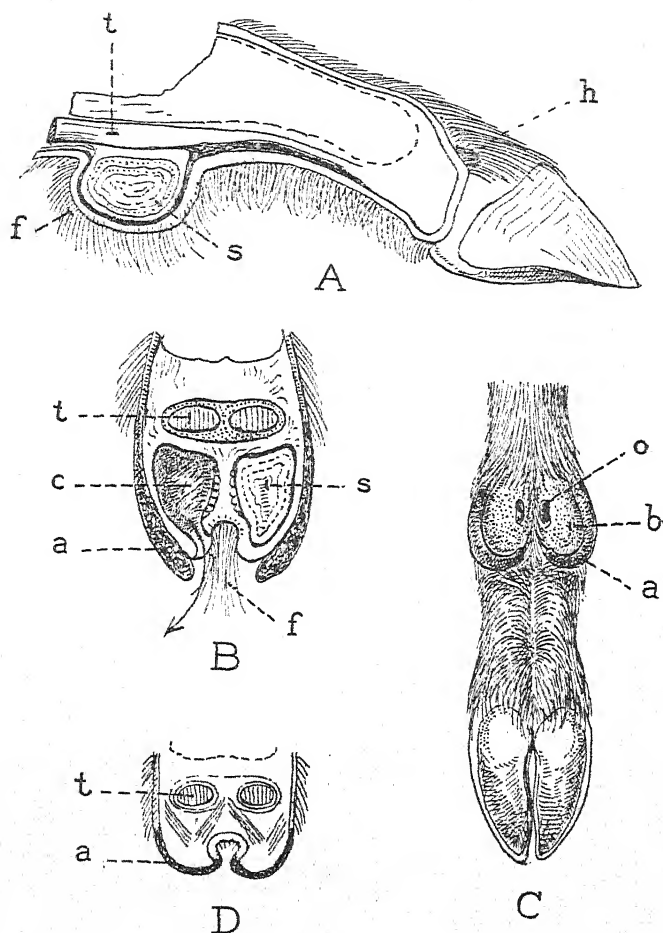
Text-fig. 118.

*Tetraceros quadricornis* ♀.

- A. Inferior view of hind foot: *fh.*, false hoof with its inner half and the adjacent skin cut away to show the glandular mass (*s.*).  
 B. Front view of the same foot showing the large horny accretion (*e.*).  
 C. The same in median vertical section.

This is the only Antelope known to me which possesses such glands. Whether these sacs are the glands that Hodgson mentioned as sometimes present in the hind feet or not I cannot say. In any case, it is quite evident that they have no sort of connection, except a functional one, with the interdigital glands of other Bovidae.

Text-fig. 119.



- A. Median vertical section of hind foot of *Tetracerus quadricornis* ♂: *t*, tendon; *h*, small horny accretion at anterior end of interungual web; *f*, fringe of hair between false hoofs; *s*, secretion within the sac shown by cutting away the partition between the two glands.
- B. Transverse section of the pastern of *T. quadricornis* ♂, through the false hoofs: *t*, tendon; *c*, glandular sac with arrow marking the orifice; *a*, false hoof; *f*, fringe of hair between the glandular areas of the false hoofs, with the partition above it; *s*, secretion within the other sac, the orifice of which is not seen.
- C. Inferior view of hind foot of *T. quadricornis* ♂: *a*, false hoof; *b*, horny but soft integument forming lower wall of gland; *o*, orifice of gland.
- D. Transverse section through the region of the false hoofs of *Tragelaphus scriptus* ♂, for comparison with B: *t*, tendon; *a*, false hoof.

*Tetraceros* is usually regarded as belonging to the Cephalophinae. I do not think, however, that the evidence for this relationship is strong. *Tetraceros* and *Cephalophus* differ widely in the structure of the feet and of the preorbital glands; but *Tetraceros* approaches *Boselaphus* in these particulars. The presence of four mammae, the absence of inguinal glands, and the size of the muffle may also be cited as corroborative evidence of this relationship. Most suggestive, too, is the presence of white patches on the pasterns, and sometimes at all events of two white specks on the cheeks in *Tetraceros*. When I noticed these marks in the living animal, before a dead one was available for examination, I felt sure that the affinities of the genus would prove to be with the Tragelaphines, a group in which these markings are extraordinarily persistent. I subsequently found that Sir Harry Johnston\* had noticed the same colour-features in *Tetraceros*, and pointed out the resemblance the genus presents to the Tragelaphines in those particulars. It is true that the horns of *Tetraceros* have no anterior crest or keel; nevertheless, they are more like the horns of *Boselaphus* than the latter are like the spirally twisted horns of the African Tragelaphines.

#### Genus BOSELAPHUS Blainv.

BOSELAPHUS TRAGOCAMELUS Pall. (The Nylghaie.)

(Text-figs. 120, 121.)

According to Owen, this species has inguinal glands; Ogilby, on the contrary, says they are absent. The two authors agree, however, as to the presence of preorbital glands; and Ogilby adds that there are distinct pedal or interdigital glands. Blanford supports Ogilby's statements.

Turner described† the preorbital gland as a slight pit immediately in front of the orbit with a small longitudinal fold of skin in front of it. In the middle of this fold (or flap) of skin "there is a small round pore, through which exudes a yellowish secretion furnished by a gland placed just underneath. The gland itself is slightly larger than a hazel-nut and is laid upon the surface of the bone without any fossa to receive it."

In an adult female example kindly sent to me by the Duke of Bedford, K.G., I found the preorbital gland marked externally by a short longitudinal slit some distance in front of the eye, the area round the slit and between it and the corner of the eye being practically naked. When opened, this slit was seen to be the orifice of a shallow elliptical depression containing some dried waxy secretion. Near the centre of the depression, but varying in position on the two sides, was a conspicuous circular hair-follicle with a hair protruding from it. There were also one or two

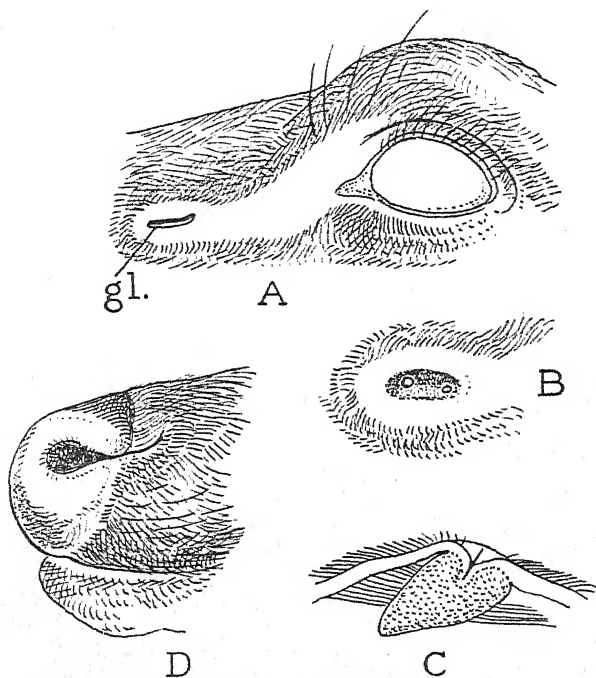
\* 'Liberia,' ii. p. 738, 1906.

† P. Z. S. 1851, p. 116.

additional but smaller hair-follicles, also varying in position. From these follicles yellow waxy secretion could be squeezed; but I could detect no special odour about the secretion. As described by Turner, the underlying glandular mass was of large size and elongated, but heart-shaped in transverse section. Its colour was yellowish.

There were two pairs of teats, but no trace of inguinal glands could be detected.

Text-fig. 120.

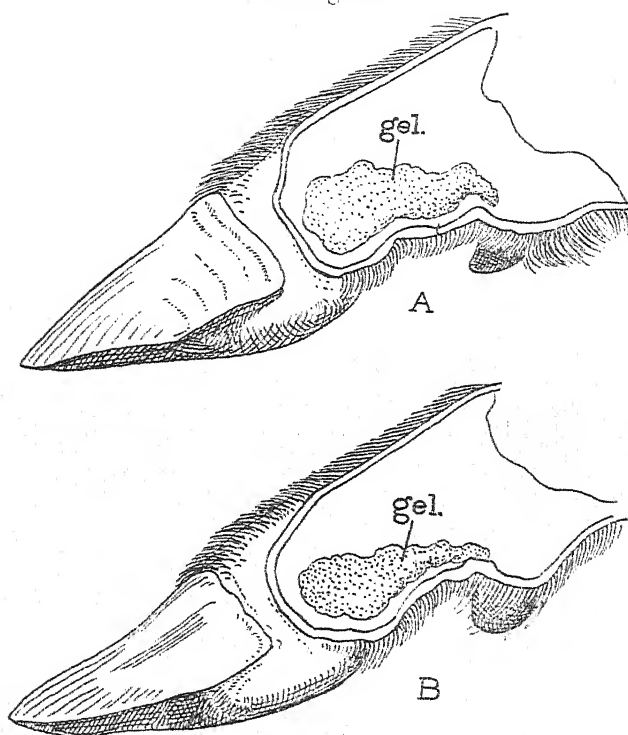
*Boselaphus tragocamelus* ♀.

- A. Portion of the face showing the eye and the orifice of the preorbital gland (*gl.*).
- B. Preorbital gland with the lid raised showing two large hair follicles.
- C. Section of the gland passing through the larger hair follicle showing the protruding bristle.
- D. Rhinarium.

The feet were constructed exactly as in other Tragelaphinæ, the interungual integument being smooth from the heels forwards towards the proximal edge of the nail in front, then inclined obliquely upwards to meet that of the anterior surface of the pastern, leaving a small smooth triangular area at the bottom of the pastern in front just above the hoofs. Between

the phalanges of the pastern was the gelatinous mass of tissue found in *Taurotragus*, *Bos*, and *Kobus*. In connection with the relationship here claimed between *Boselaphus* and *Tetraceros*, it was especially interesting to note that the skin between the false hoofs of the hind feet was white, thick, and highly glandular, the hairs being packed with secretion, smelling like the fat of tallow candles.

Text-fig. 121.

*Boselaphus tragocamelus* ♀.

- A. Median vertical section of hind foot: *gel.*, gelatinous mass between the phalanges.  
 B. The same of the front foot.

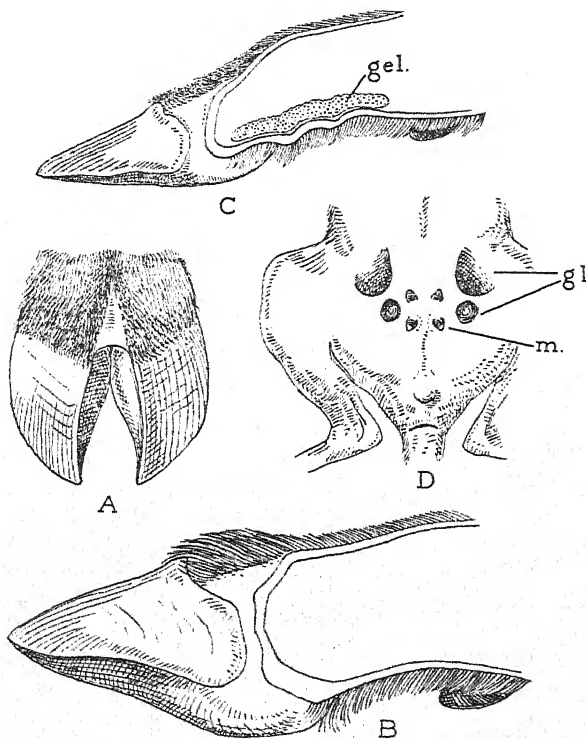
This specimen proves that Owen's statement about the inguinal glands and Ogilby's statement, apparently copied by Blanford, about the pedal glands are alike erroneous. It further shows that the prevalent view as to the kinship between *Boselaphus* and the African *Tragelaphines* is correct, and affords no support whatever to the suggestion found in Max Weber's 'Säugethiere,' pp. 675-676, that *Boselaphus* probably belongs to the *Bubalinae* and not to the *Tragelaphinae*.

Genus *TRAGELAPHUS* Blainv.*TRAGELAPHUS SCRIPTUS* and its subspecies.

(Text-figs. 116, C, p. 922, &amp; 122, C, D.)

Owen records the absence of preorbital and the presence of inguinal glands in specimens of the genus he identified as *Antelope scripta* and *A. sylvatica*. W. L. Sclater, however, says that the preorbital gland is "present, but small and with a very small aperture," in the genus *Tragelaphus*, with which *Limnotragus* was included.

Text-fig. 122.



- A. Anterior aspect of foot of young specimen of *Taurotragus oryx*.  
 B. Median vertical section of foot (? front or hind) of adult female of *Taurotragus oryx* (dried).  
 C. Median vertical section of front foot of *Tragelaphus scriptus* ? *roualeyni*: *gel.*, gelatinous mass between the phalanges (dried).  
 D. Inguinal region of female foetal example of *Tragelaphus scriptus* (subsp. ?) from Unyoro: *gl.*, the two inguinal pouches; *m.*, mammae.

The only entire specimen of this genus that I have examined was a female foetal example, of which I do not know the subspecies,



from Unyoro in Uganda, which was preserved in spirit and kindly given to me by Dr. Cuthbert Christy, F.Z.S. It had no preorbital glands, but two pairs of well-developed inguinal glands resembling those of *Cervicapra redunca*, the pockets of the anterior pair being shallow but wide-mouthed, and those of the posterior pair deeper with circular orifice somewhat less in diameter than the diameter of the pocket itself. Between the orifices of the inguinal pockets were the two pairs of teats. The early development of the inguinal glands is a fact of considerable interest.

There was no trace of pedal glands and only a very shallow and short depression on the anterior surface of the fetlock close to the base of the hoofs. The interungual area was naked as in *Taurotragus*, and the web was deep, extending from near the proximal end of the front of the hoof to the heels.

I have also examined the head, feet, and skin of the inguinal region of a young male of *T. scriptus scriptus* from French Guinea, presented to the Society by Mr. Fenwick Owen. This material was preserved in alcohol. The feet were constructed as above described, and there was no preorbital gland. There were two pairs of teats, but only a single pair of inguinal glands, each consisting of a pouch about an inch deep opening by an orifice some distance away from, and in front of, the mammæ of the anterior pair (text-fig. 116, C, p. 922). I think it probable that these glands correspond to the deep posterior pair, and not to the shallow anterior pair observed in the foetal example above described.

I also received from Mr. E. Gerrard the dried front and hind feet of a Bushbuck, probably belonging to *T. scriptus roualeyni*, which also had no trace of pedal glands; but in which I was able to discover the shrivelled remains of the vascular gelatinous (fatty) mass lying along the back of the pastern between the true and false hoofs, which has been already described in *Cervicapra redunca* and *Adenota kob*.

#### TRAGELAPHUS ANGASII Angas.

(The Inyala.)

Of this species I received from Messrs. Rowland Ward, Ltd., a single dried foot of a male, which differed in no important respects from the foot of *T. scriptus*, except that the naked shallow depression at the base of the hoofs on the front of the pastern was obliterated and the hoofs themselves were shorter with higher heels, suggesting the habit of walking on firmer ground.

#### Genus LIMNOTRAGUS ScL. & Poc.

##### LIMNOTRAGUS GRATUS ScL.

As stated above, W. L. Sclater says the preorbital gland is present in the southern race of *L. gratus*, namely, *L. gratus selousi* Roths., the true Sitatunga.

I have examined no dead examples of this genus in a fresh state, but examples of the typical *L. gratus* and of *L. gratus selousi* living in the Gardens show no trace of a preorbital gland, nor of pedal glands, the widely splayed hoofs making observation of the absence of the pedal glands comparatively easy. The feet appear to resemble those of *Tragelaphus*, apart from the length of the hoofs and the nakedness of the back of the pasterns. Max Weber (Die Säug. p. 35, fig. 31, 1904) has figured the inguinal region of a male and female of *L. gratus*, showing the presence of four mammae and of a single pair of small, almost aborted inguinal sacs, with orifices remote from and well in advance of the anterior mammae. These obviously represent the larger inguinal sacs seen in the specimen of *Tragelaphus scriptus scriptus* above described. It may further be noted that the glands as figured by Weber closely resemble in size and position the single minute inguinal sac seen on one side in the young example of *Adenota kob* (p. 916): both are suggestive of a larger sac in process of suppression.

Genus STREPSICEROS H. Sm.

STREPSICEROS STREPSICEROS Pall.

(The Greater Kudu.)

According to Owen, this species has inguinal pits but no preorbital gland. Ogilby agrees with Owen as regards the absence of preorbital glands and the presence of inguinal glands, and adds that pedal glands are also absent. He also records the presence of four mammae. W. L. Slater, however, says that the preorbital gland and its orifice are small. I have examined no example of this species, but the available data suggest that *Strepsiceros* resembles *Tragelaphus* or *Limnotragus* in the matter of cutaneous glands, as it is well known to do in most other structural characters, apart from the slight difference exhibited in the structure of the horns. It is impossible, however, to guess whether this genus has inguinal glands like those of the foetal *T. scriptus* (subsp.?) or the young *T. s. scriptus*, described above, or like those of *Limnotragus gratus* figured by Max Weber. I suspect, however, that they will prove to resemble in size and number those of *T. s. scriptus*.

Genus BOOCERCUS, THOS.

BOOCERCUS EURYCEROS Ogilby.

(The Bongo.)

In an old skin of this species which Mr. Gerrard allowed me to examine, I found the feet to be constructed as in *Taurotragus*, there being no trace of glands and the interungual web being naked throughout its extent. I could detect no trace of inguinal glands, but found two pairs of teats.

The apparent absence of inguinal glands in this genus and in

*Taurotragus* and their presence in *Tragelaphus* and, as is alleged, in *Strepsiceros* are quite in accordance with the view that *Boocercus* and *Taurotragus* are more nearly allied to one another than either is to *Strepsiceros* or *Tragelaphus*, a view supported by the terminally tufted tail and the presence of horns in the female in the two former genera.

### Genus TAUROTIRAGUS Wagn.

TAUROTIRAGUS ORYX Pall. (The Eland.)

(Text-fig. 122, A, B, p. 929.)

This species, according to Owen, who quotes it as *oreas* and *canna*, has neither preorbital nor inguinal pits. W. L. Sclater, however, says that the preorbital gland is small, "with a very small circular opening in front of the eye in a narrow bare triangular space." In two young male examples examined by me, I could find no trace of preorbital gland or of inguinal or pedal glands. The pedal glands were also entirely absent on a foot of an adult kindly supplied to me by Messrs. Rowland Ward, Ltd.

The feet are constructed as in the genus *Bos*, the entire interungual area being naked, the integument that joins the hoofs together forming a deep "web" extending forwards from the heels where it is thickest, to the anterior portion of the pastern only a short distance above the proximal margin of the front of the hoof, so that the hoofs are susceptible of but little separation.

By their glands and other external features the genera of this section may be grouped and contrasted as follows:—

- |   |  |
|---|--|
| a. A well-developed preorbital gland opening by a longitudinal valvular slit; horns short, not spirally twisted, present only in the male (tail not terminally tufted; no inguinal glands). |  |
| b. Preorbital gland relatively large; horn not crested; a pouch-like gland in each false hoof of the hind leg, &c. ....   | <i>Tetraceros.</i>                             |
| b'. Preorbital gland relatively small; horns crested basally; skin between posterior false hoofs highly glandular .....   | <i>Boselaphus.</i>                             |
| a'. No preorbital gland; horns longish, spirally twisted.   |  |
| c. Inguinal glands present; tail hairy throughout; no horns in female .....   | <i>Tragelaphus, Limnotragus, Strepsiceros.</i> |
| c'. No inguinal glands; tail terminally tufted; horns present in both sexes .....   | <i>Boocercus, Taurotragus.</i>                 |

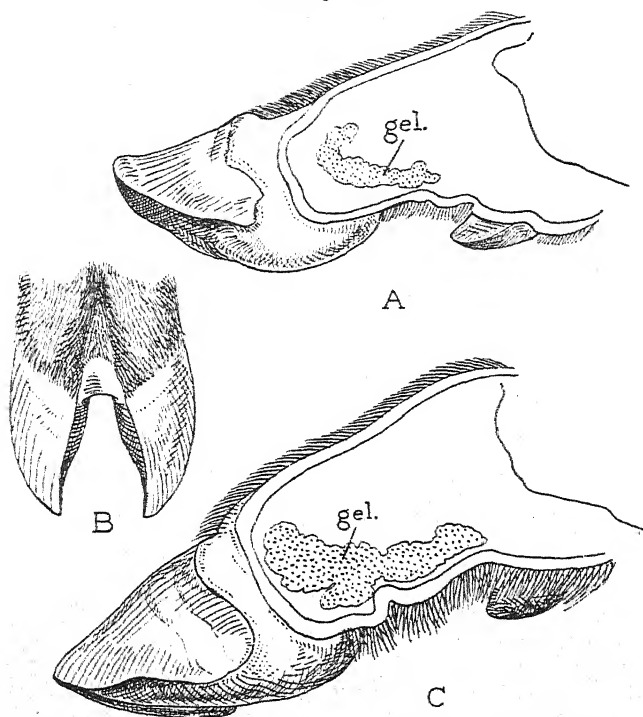
### Subfamily BOVINÆ.

Genus *Bos* Linn. (Text-figs. 123, 124.)

It is agreed on all hands that preorbital, inguinal, and pedal glands are absent, and that two pairs of mammae are present in all the species of Bovinæ, whether they be referred to the one genus *Bos* or the several genera *Bos*, *Bibos*, *Poephagus*, &c. In these respects Cattle are indistinguishable from the large Tragelaphine Antelopes *Taurotragus* and *Boocercus* and from the larger forms of Cervicaprinæ like *Kobus ellipsyprymnus*. They also resemble them in the structure of the feet, the interungual

membrane being naked and continued straight backwards from a point near the anterior proximal edge of the hoof to the heels, forming a rectangular continuation on the middle line in front and behind with the integument of the anterior and posterior surfaces of the pastern respectively.

Text-fig. 123.



- A. Median vertical section of foot of *Bos sondaicus*, three days old: *gel.*, gelatinous mass between the phalanges.  
 B. Anterior aspect of the same foot.  
 C. Median vertical section of foot of calf of *Bos taurus*; *gel.*, gelatinous mass between the phalanges.

I have verified this fact upon feet of specimens of the following species:—

*Bos taurus* L. (Ox); fore and hind feet of a calf given to me by Mr. R. E. Holding.

*Bos indicus* L. (Zebu); feet of adult male that died in the Gardens.

*Bos frontalis* Lambert (Gayal); ditto.

*Bos gaurus* H. Sm. (Gaur); foot given to me by Mr. R. E. Holding.

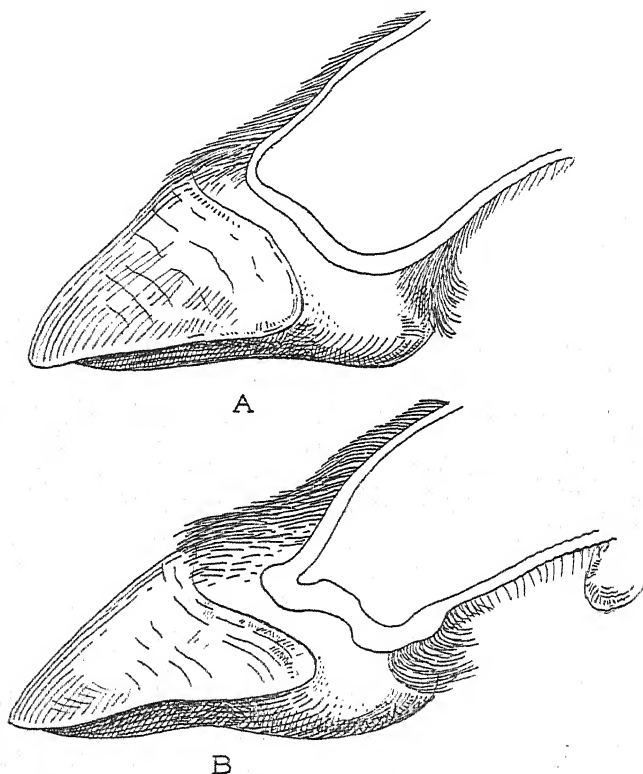
*Bos sondaicus* Schleg. & Müll. (Banting); calf four days old that died in the Gardens.

*Bos grunniens* (Yak); a female specimen.

*Bos caffer* Sparrm. (African Buffalo); dried foot lent to me by Rowland Ward, Ltd.

*Bos bubalus* L. (Indian Buffalo); ditto.

Text-fig. 124.



A. Median vertical section of foot of *Bos bubalus* (dried).  
B. The same of *Bos caffer* (dried).

In fresh specimens there is always a mass of vascular gelatinous tissue between the penultimate phalanges of the pastern, corresponding to that which is found along the posterior inner surface of the pastern in fresh specimens of *Adenota kob*, *Cervicapra redunca*, *Taurotragus*, *Boselaphus*, etc.

In the feet of the two Buffalos mentioned above I found the interdigital integument much thicker in *B. caffer* than in *B. bubalus*, and the former had a deeper depression on the front

of the fetlock above the hoofs than the latter, the interungual web not extending so far to the front and allowing the hoofs to be rather more widely spread.

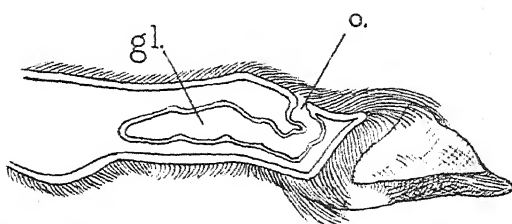
### Family ANTILOCAPRIDÆ.

ANTILOCAPRA AMERICANA Ord. (The Prongbuck.)

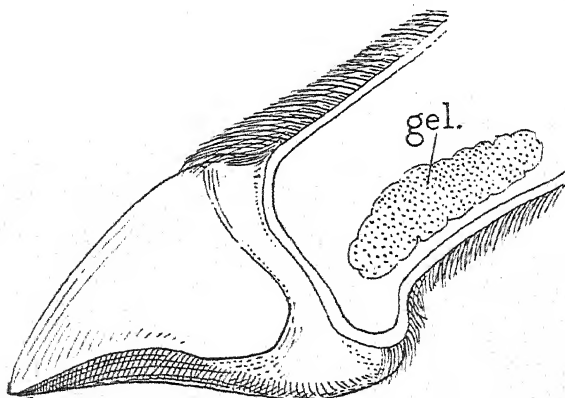
(Text-fig. 125, A.)

In his paper upon the anatomy of this species (P.Z.S. 1870, p. 340), Dr. Murie summarised his own observations and those

Text-fig. 125.



A



B

- A. Median vertical section of front foot of prematurely born example of *Antilocapra americana*: *gl.*, pedal gland; *o.*, its orifice.  
 B. Median vertical section of hind foot of *Giraffa camelopardalis*, three weeks old; *gel.*, gelatinous mass between the phalanges.

of previous authors on the cutaneous glands as follows:—(1) no preorbital or inguinal glands; (2) a gland an inch and a half

below the ear which exudes a yellow glutinous secretion with a strong goaty odour; (3) an unpaired dorsal gland six or eight inches in front of the tail; (4) a gland on each side of the tail above the ischiatic prominence; (5) a gland on the posterior aspect of each hock; (6) interdigital glands on all four limbs.

My observations on this species were limited to a prematurely born foetus. On this I could find no trace of the glands below the ears or on the hocks or on the ischia, except for the crease of skin at the root of the tail on each side. The dorsal gland was in a rudimentary condition, the hairs on each side of the spine of the lumbo-sacral area showing a black spot and being slightly stuck together.

In view of the absence or rudimentary condition of the glands mentioned, it was interesting to find the pedal glands highly developed. They opened by a small circular orifice on the front of the pastern some distance above the base of the hoofs. The orifice led into a long and spacious gland directed at first downwards towards the hoofs, then sharply curved upwards along the posterior wall of the pastern, occupying almost the entire space between the phalanges of the feet, nearly as far up as their articulation with the cannon-bone. These glands, present on all four feet, were crammed full of white cheesy secretion. They resembled on a very large scale the glands of Sheep more than the glands of any of the Bovidae or Cervidae, although the orifice was situated higher up the pastern than in *Ovis*, recalling in this particular the orifice of such a Deer as *Capreolus*. It was noticeable, too, that there was no depression on the front of the pastern for the orifice to open upon. The hoofs were united by a very deep and continuously hairy web, extending from the heels as far forwards as the anterior proximal margin of the hoofs.

#### Family GIRAFFIDÆ.

GIRAFFA CAMELOPARDALIS Linn. (The Giraffe.)

(Text-fig. 125, B.)

According to Ogilby, the Giraffe has neither preorbital nor inguinal glands, but has small interdigital fossæ and four mammae.

A young specimen, three weeks old, that died in the Zoological Gardens, presented the characters mentioned by Ogilby except that there was no trace of "interdigital fossæ," the feet being completely webbed, with low heels and no trace of a depression on the front of the pastern. The interungual integument, moreover, was quite naked from front to back, as in Bovine and Tragelaphine Ruminants, and the same gelatinous mass of tissue was present between the penultimate phalanges of the pastern as is found in the latter animals.

There was a thick pad of hairs over and below the knees; but I could detect no evidence of glandular activity in the underlying skin, there being plenty of underwool but no secretion at the base

of the long hairs of the pad. The same pad, I noticed, was well developed in a foetal Giraffe taken from its mother that died some four years ago in the Gardens (see F. E. Beddard, P. Z. S. 1906, ii. p. 630, fig. 109).

The horns of the three weeks old specimen, which were relatively as large as in the adult, had no connection, apart from contact, with the skull, a fact already recorded by Sir Ray Lankester (P. Z. S. 1907, p. 101).

### Family MOSCHIDÆ.

#### MOSCHUS MOSCHIFERUS Linn. (The Musk-Deer.)

(Text-fig. 126.)

The peculiar musk-gland of the male of this species has been described by many authors, and I have nothing to add to what has already been said of this organ\*. Ogilby and Hodgson state that the preorbital and pedal glands are absent. Flower† confirms this, saying "nor were there any interdigital glands on either feet, the depressed space between the toes, where the glands usually open, being covered with hair." Brandt also described a gland on the outer side of the thigh in the male‡; and Hodgson discovered a gland opening on each side of the tail in that sex§. Neither the femoral nor caudal glands were found by Flower in the female example dissected by him.

I have only seen one example of this species, a male from Chamba presented to the Society by Major G. S. Rodon, F.Z.S.; at the time of its death I merely noted the structure of the feet and the absence of the preorbital gland. On the front feet it was very obvious that the long hairs of the interdigital depression were stuck together with a brown sticky substance, having a decided but indescribable smell and indicating considerable activity of the sebaceous glands. On the hind feet there was no such secretion, the hairs being clean and separable. The depression between the phalanges of the feet in this species is deep, the integument of the upper and under sides meeting at an acute angle to form a web which extends nearly as far as the heels of the hoofs; but on the hind feet the webbing is wider and not so thick as on the front feet, so that the hoofs of the former are capable of being rather more widely distended. The entire interdigital and interungual area is thickly covered with long hairs the tips of which overlap the proximal portion of the hoofs to a considerable extent.

On the dried skin I find no trace of the femoral gland described

\* The scent of the secretion of this gland when fresh is decidedly unpleasant, with a peculiar pungent urinary odour. It bears no sort of resemblance that I can detect to the prepared "musk" of commerce. This is one of the criticisms that may be made on Mr. Beddard's perhaps satirical suggestion ("Mammalia" in the Cambridge Natural History, p. 13, 1902) that the musky scent of this Deer may be mimetic, in the sense of frightening its enemies by suggesting the proximity of Crocodiles.

† P. Z. S. 1875, p. 159 &c.

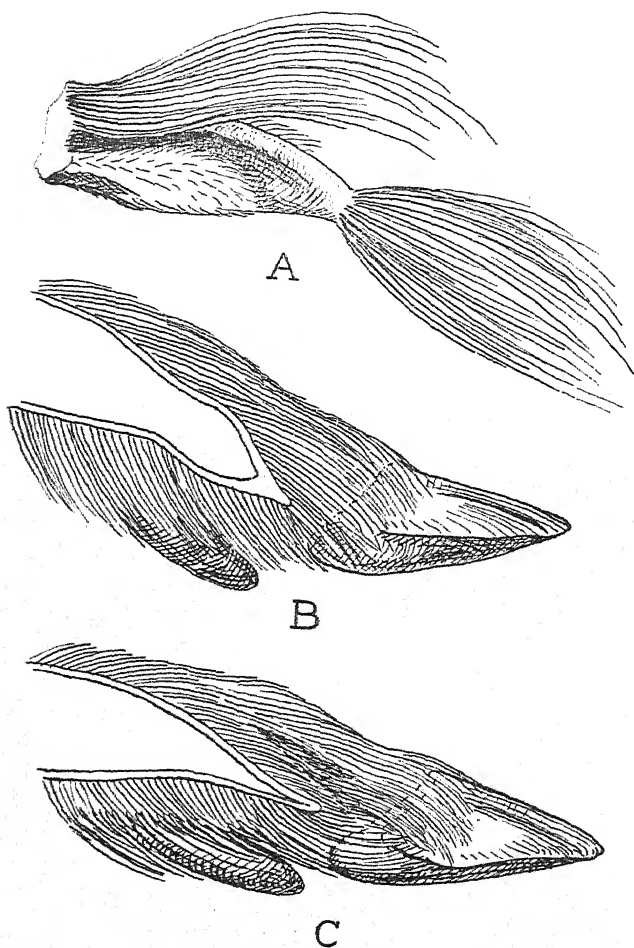
‡ Bull. Sci. Acad. St. Pétersb. i. p. 174, 1836.

§ J. A. S. Bengal, x. p. 795, 1841.



by Brandt nor of the so-called calcic (? tarsal or metatarsal) gland mentioned by Hodgson. The tail, however, is very peculiar. It is completely buried in the long hairs of the anal region and is for

Text-fig. 126.



*Moschus moschiferus* ♂.

- A. Lateral aspect of tail (dried).
- B. Median vertical section of front foot (dried).
- C. The same of hind foot (dried).

the most part naked. Its tip, however, is furnished with a large tuft, and its naked upper and lateral portions are overhung by long

hairs projecting backwards from its base on the upper side. Just behind the anus on the lower side there is a mat of short hairs which extends upwards laterally so as to cover the lower half of the side of the tail. Just above this the lateral surface of the tail is scooped out longitudinally, forming a wide gutter, which is filled with yellow crumbly secretion, and this extends over the summit of the tail and almost to its apex, both above and at the sides. Before the skin became shrunken with drying, it is probable that it was full and flaccid, and that the wide gutter above described had the appearance of a narrow integumental slit such as Hodgson figured.

From the great development of the caudal gland as well as of the preputial gland in the male of the Musk-Deer, it may be inferred that the females seek the males at the rutting season.

One other point may be noted: both Ogilby and Hodgson declare that this Deer has two pairs of teats. Flower, on the contrary, found only a single pair on the female he examined, and I noted that the male above mentioned also had but one pair.

#### Family CERVIDÆ.

In describing the cutaneous scent-glands of the Deer I have not taken into account the statements made by Fitzinger in his diagnoses of the genera of this group (SB. Akad. Wien, lxxviii. pp. 348-362, 1873), because many of them are contradicted by the plainest facts. He says, for example, that *Rangifer* has no tarsal gland and that *Cervulus*, *Axis*, *Hyelaphus porcinus*, *Dorcylaphus americanus*, *Mazama nemorivagus*, and *Dama* have no pedal glands. Since these glands are extremely well developed in all these Deer, it is clear that no reliance is to be placed on this author's statements as to their absence in other species.

From the works of previous authors it is well known that one or more pairs of the following glands are present in all species of this family:—

1. Pouch-like, shallower or deeper, preorbital glands, which are apparently absent only in *Capreolus*.
2. Frontal glands, which are well developed in some species of the Muntjac group and, according to Weber, in the Sambar.
3. Tarsal glands, consisting of a hair-covered patch of thickened skin on the inner side of the tarsus or hock and especially characteristic of the American Deer.
4. Metatarsal glands, which usually resemble the last structurally, but are placed on the outer side of the metatarsus or cannon-bone of the hind leg at a varying distance below the hock.
5. Pedal glands, which when well developed consist of a large or small cleft or pouch on the front of the pastern usually of the hind foot only, more rarely of the front as well.

Inguinal glands do not exist, and there are always two pairs of teats.

## Genus CERVUS Linn.

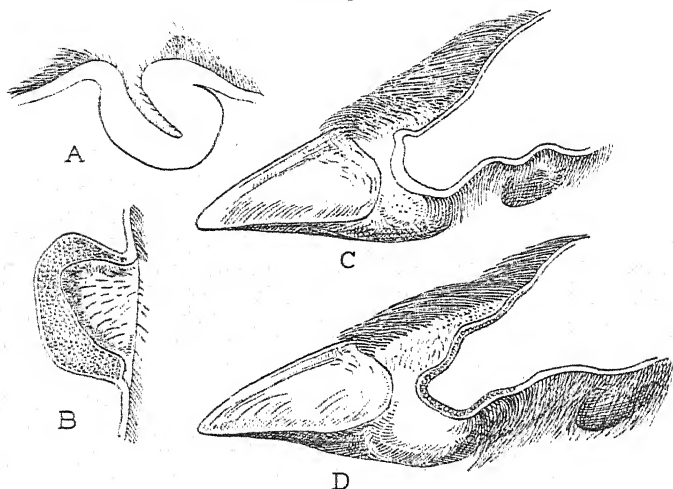
## CERVUS (CERVUS) MARAL Ogilby.

## (The Caucasian Red Deer.) (Text-fig. 127.)

In an old Stag of this species that died in the Gardens the orifice of the preorbital gland formed a subvertical S-shaped slit at right angles to the long axis of the eye-aperture. The gland itself was a simple but deep infolding of enormously thickened skin, the pocket being scantily lined with short hair and filled with a yellow waxy secretion.

The metatarsal gland was represented by a thick mat of hair paler in colour than that of the rest of the leg. The area beneath this mat was nowhere naked, as it is in *Aris aris*.

Text-fig. 127.

*Cervus (Cervus) maral.*

- A. Transverse section through preorbital gland.
- B. Longitudinal section through the same.
- C. Median vertical section of front foot.
- D. The same of hind foot.

On the front hoof the integument of the anterior surface of the pastern formed a rather shallow depression uniformly clothed with hair almost to the bottom. The interungual integument was very thick and horny throughout its extent, forming a strong but elastic union between the hoofs. Along the back of the pastern up to the false hoofs the skin was also moderately thickened; but I could detect no evidence of any special glandular activity in the skin of the front feet.

On the hind feet the interdigital depression on the anterior side of the pastern was much deeper, the integument being much more steeply inclined backwards and downwards towards the heels, the

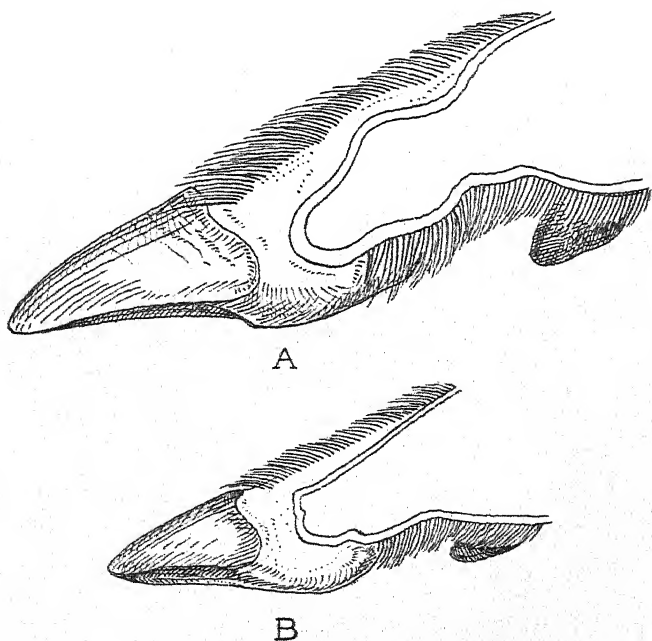
hoofs being joined together by a moderately deep and strong smooth tie just above the heels. The integument of the deeper portion of the interdigital depression was almost naked, being merely sparsely clothed with short hair, and instead of forming a continuous and level surface was sinuous or slightly folded, so that the depression was somewhat deeper above and below than in the middle. In section it was speckled with a layer of small dark spherical glands, which extended not only over the skin of the depression itself but round the interungual tie and some little distance above the heels on the back of the pastern. These dark specks, clearly visible to the naked eye, sharply define the position of the skin with active glands from the rest.

The main differences, then, between the front and hind feet are the presence of a deeper nearly naked interdigital depression, of a shorter and weaker interungual web, and of more highly developed sebaceous glands in the latter than in the former.

CERVUS (CERVUS) ELAPHUS Linn. (The Red Deer.)  
(Text-fig. 128, A.)

According to Ogilby, *C. elaphus* has distinct and movable pre-orbital glands and large pedal glands. Hodgson described the

Text-fig. 128.



A. Median vertical section of hind foot of *Cervus (Cervus) elaphus*.  
B. The same of *Cervus (Rucerrus) duvanceli*.

preorbital glands as moderate in size and mobility and S-shaped, the pedal glands as large but doubtfully present on all four feet; and added that the metatarsal gland is posterior and external. I am indebted to Sir Claud Alexander, Bt., F.Z.S., for the front and hind feet and the mask of a freshly killed Stag from Scotland.

The preorbital gland resembled that of *C. maral*, except that the orifice, when closed, formed a long slit, lightly concave upwards and inclined obliquely at a very obtuse angle to the long axis of the aperture of the eye.

The feet also were very like those of the Caucasian species, except that the horny heels of the front hoofs were united below the strong cutaneous heel-tie and a larger area of the deep portion of the interdigital depression was very scantily clothed with short hair. On the hind foot the depression, as in *C. maral*, was considerably deeper and was divided by a transverse bridge into a smaller upper portion and a larger lower portion, both better marked than in that species.

#### CERVUS (CERVUS) CANADENSIS EHL.

(The Canadian Wapiti.)

The glands of this species resemble in all essential respects those of *C. elaphus* and *C. maral*.

In an old male that died in the Gardens the orifice of the preorbital gland was inclined at an obtuse angle to the axis of the ocular aperture; the pocket was deep with nearly naked walls; the skin of the bottom at its deepest part just in front of the orbit was very thin, the thickest part being close to the orifice, especially on its anterior side. The secretion, which was very dry, smelt like green grass just beginning to decay.

The metatarsal gland consisted of thickened skin completely covered with hairs, which were white at the base and clogged with secretion smelling like a pen of Domestic Sheep.

The feet in section were very like those of *C. elaphus* and *C. maral*, except that the depression on the front of the pasterns was shallower and the nail of the hoofs shorter. The heels of the front hoofs were separated as in *C. maral*, not united as in the example of *C. elaphus* examined.

According to Hodgson, the Hangul or Cashmere Stag (*Cervus cashmirianus*), which he quotes as *C. wallichii*, and the Shou (*Cervus affinis*) agree with *C. elaphus* in their cutaneous glands.

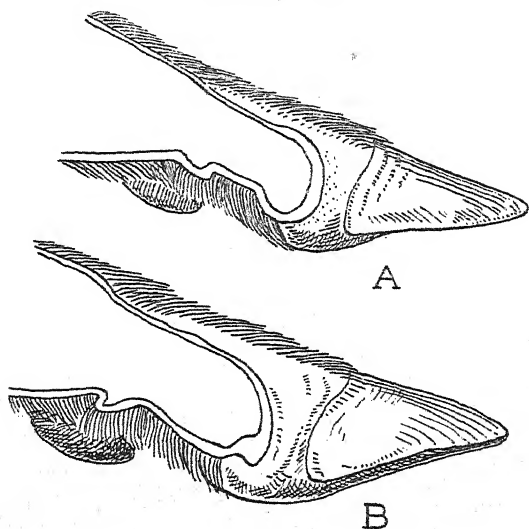
#### CERVUS (PSEUDAXIS) SIKA Temm. (Japanese Deer.)

(Text-fig. 129.)

Two young male examples, about eighteen months old, agreed closely in a general way with *C. maral* and *C. elaphus*, except that the preorbital glands were much less developed, the infolding being comparatively quite shallow. The metatarsal gland was marked by a large elliptical white patch, consisting for the most part of

hairs with white tips. The bases of the hairs were covered with adhesive secretion and the underlying skin was markedly thick and glandular. In both the front and the hind feet the anterior interdigital depression was naked and nearly hairless in its deeper portion, but in the hind foot it was not subdivided into an upper and a lower portion, which are so well marked in *C. elaphus*, the floor of the depression sloping gradually and evenly downwards and backwards from the tarso-metatarsal joint as in the front leg, and the interdigital web was developed to about the same extent in the two feet. In section the skin of this area showed no especial signs of glandular activity.

Text-fig. 129.

*Cervus (Pseudaxis) sika.*

A. Median vertical section of front foot. | B. Median vertical section of hind foot.

Although, on the evidence supplied by the antlers, Mr. Garrod believed *Pseudaxis* to be nearly related to *Dama*, the structure of the feet affords no support to this view.

*Pseudaxis sika* readily interbreeds with *Cervus elaphus*.

#### CERVUS (RUCERVUS) DUVAUCELI Cuv.

(The Swamp-Deer or Bárasingha.) (Text-fig. 128, B, p. 941.)

Hodgson, who refers this species to two genera under the names *Rucervus elaphoides* vel *duvauceli* and *Procervus dimorphe*, says that the preorbital glands are moderate, and moderately movable in the former, medial and vertical in the latter, that the pedal

glands are absent, and that the presence of metatarsal glands is doubtful.

In a young example, two months old, the preorbital gland was scarcely developed, and consisted of little more than a shallow naked channel running obliquely downwards and forwards from the corner of the eye. There was no trace of metatarsal gland; nor can I detect this gland in living examples of the species.

The feet were very similar to those of the previously described species. On the front leg the skin of the anterior surface of the pastern descended somewhat abruptly downwards and backwards just above the hoofs, meeting at an acute angle the portion forming the heel-tie which extended for a longer distance in a direction parallel to the sole of the foot than in the other species. There was no naked area along the middle line of the front of the pastern: on the hind foot, however, this naked area was well marked all the way up the front of the pastern, which was but little depressed and showed no indication of being deeper above and below than in the middle. The interungual integument or web formed an obtuse angle with that of the front of the pastern and a right angle with that of its posterior surface, the heel-tie being long as in the front foot. On the posterior side of the pastern the hairs did not extend between the heels, as they did for a short distance in the case of the previously described species.

It is important to note the very slight differentiation of the preorbital gland in this young specimen, and also its smaller size in the eighteen months old examples of *C. sika* as compared with that of the adult. From these facts it may be inferred that the gland in question develops with age in these Cervidae. They are quite large, however, in newly born Muntjacs (*Cervulus*).

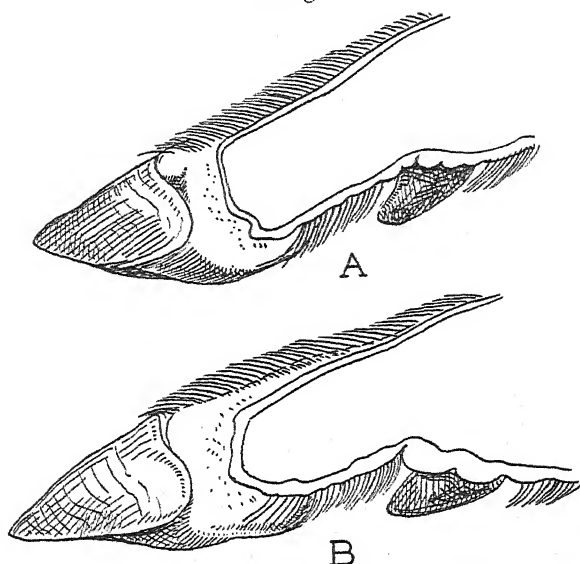
CERVUS (PANOLIA) ELDI Guthr. (The Thameng or Thamin.)  
(Text-fig. 130.)

In a very old male of this species the preorbital gland was well developed, the invagination being about one inch deep at its deepest part above, the direction of the long orifice, when closed, being intermediate between that of *C. maral* and *C. elaphus*. The metatarsal gland was marked by a patch of hairs paler than those of the rest of the leg, with their bases clogged with black secretion, the underlying skin being thick and markedly glandular to the naked eye.

There was scarcely any depression on the front of the pastern of either the front or the hind foot. On the front foot the very shallow depression was hairy throughout as in *C. duvauceli*, without the naked area seen in *C. maral*, *elaphus*, and *sika*; and even on the hind leg this naked area was of very small extent. Since the skin of this area did not slope downwards and backwards between the hoofs in front, it resulted that the interungual tie or web was of much greater extent than in the other species, the feet,

in section, being constructed very much as in the Tragelaphine Bovidae; but, as in the other species of Cervidae hitherto described, the interungual web was quite naked. The portion of this web which formed the heel-tie was wider than in the other Deer, giving greater distensibility to the hoofs, and the skin surrounding the false hoofs was naked, although the back of the pastern was normally hairy between the false hoofs and the heels\*.

Text-fig. 130.

*Cervus (Panolia) eldi.*

A. Median vertical section of front foot. | B. Median vertical section of hind foot.

### Genus ELAPHURUS M.-Edw.

#### ELAPHURUS DAVIDIANUS M.-Edw.

(The Milou or Père David's Deer.)

According to Mr. Lydekker ('Deer of all Lands,' pp. 233-237) the preorbital gland is large, the metatarsal gland covered with hair and situated in the upper third of the cannon-bone, and the foot-glands and tarsal glands absent in this species.

Examination of a dried skin in the British Museum has enabled me to verify these statements, and to add to the information supplied by Mr. Lydekker the fact that the interungual integument or web is naked as in *C. elaphus*, *maral*, *sika*, *eldi*,

\* In one race of this species the whole of the back of the pastern is naked as in *Limnotherus*.



and *duvauceli*. Apart from the greater length of the false hoofs, the feet of *Elaphurus* seem to differ from those of the species just cited in having the integumental groove on their upper or anterior surfaces covered with short hair like that of the rest of the foot, instead of being naked at the bottom.

Opinions of authors as to the systematic position of this Deer are divided in accordance with the value attached to particular characters. Those, like Gordon Cameron and Lydekker, who rely mainly upon the antlers, place *Elaphurus* with the American Deer; Brooke, on the contrary, depending largely upon the structure of the lateral metacarpals, maintained that *Elaphurus* was an aberrant type of the group to which *C. elaphus*, *dama*, *unicolor*, and others belong.

The structure of the interdigital area of the pastern—that is to say, the absence of the glandular pouch and depression on the hind leg, and the smoothness of the interungual integument—and the high position of the metatarsal gland completely bear out Sir Victor Brooke's opinion as to the affiliation of *Elaphurus* with the Old World Deer, especially the Oriental types (*cf. infra*, pp. 969–970).

In opposition to Mr. Cameron's view that *Elaphurus* is not related to the Old World Deer, the Marquis of Hamilton ('Field,' July 1910, p. 199) pointed out that hybrids between *Elaphurus* and *Cervus* have been bred in Paris and that one of these hybrids formed fertile unions with both parent stocks at Woburn. This is an important piece of evidence in favour of relationship between the two genera.

### Genus *RUSA* Ham. Smith.

*RUSA UNICOLOR* Bechst. (The Sambar.)

(Text-fig. 131.)

According to Ogilby, this species has distinct and movable preorbital glands and large pedal glands, the same epithets being applied to them as to those of *C. elaphus*, suggesting identity of development and structure. Hodgson supplements this description by saying that the preorbital glands are very large and completely reversile, that the pedal glands are large and present on all four feet, and that the metatarsal gland is posterior and external. According to Blanford, however, Hodgson says the interdigital glands are wanting. I have seen one old male example of this species.

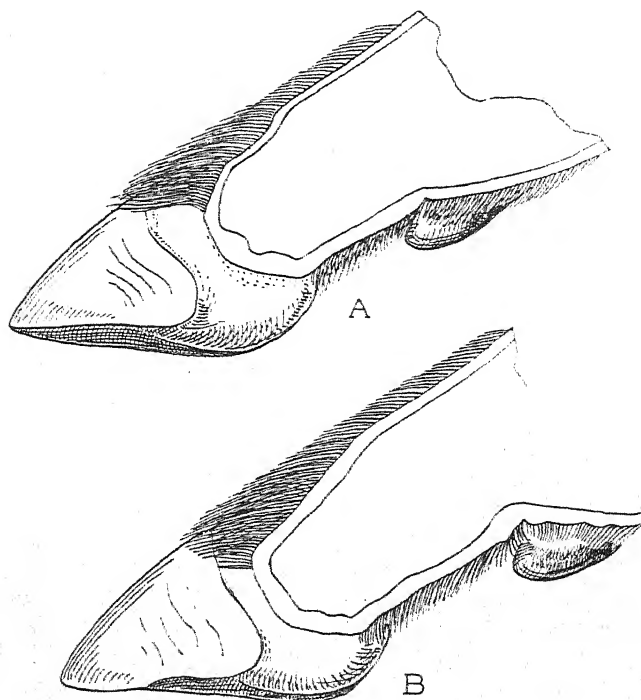
The preorbital gland was a large and deep, naked invagination half filled with a quantity of waxy secretion with a strong but indescribable odour. The integument at the bottom of the pouch was thin and apparently not glandular; but round the orifice, especially anteriorly, it was much thickened, and it was here apparently that the secreting area was concentrated.

The supraorbital gland, mentioned by Weber as present in

*Rusa equina*, I did not find; and no living Sambar that I have seen has any gland on the forehead comparable in development to that of the Muntjac (*Cervulus*).

The metatarsal gland was represented by a tuft of hair, which, as in *Elaphurus* and *Cervus*, completely covered the underlying skin. No evidence, however, of the glandular activity of the skin was supplied by secretion at the base of the hairs.

Text-fig. 131.



*Rusa unicolor.*

A. Median vertical section of front foot. | B. Median vertical section of hind foot.

Neither on the front nor the hind feet was there a trace of interdigital depression such as is seen in the Axis and Hog Deer. The front of the pastern in both feet was only shallowly depressed and was covered with hair as in *Elaphurus*, and the interungual web was quite naked as in the latter and in the typical Old World Elaphine Deer.

The difference in the structure of the hind feet between the Sambar and the Axis justifies the generic separation of the two; with this is correlated the nakedness of the metatarsal gland in

the latter animal and its hairy clothing in the former. On the other hand, although the Sambar resembles the Barasingha (*C. (Rucervus) duvauceli*), the Thamin (*C. (Panolia) eldi*), and the Japanese Deer (*C. (Pseudaxis) sika*) in the structure of the feet, it may be generically distinguished from these as well as from the typical Elaphine Stags by the longer bushier tail and the extension of the muffle as a distinct broadish rim of moist hairless skin beneath the nostril.

According to the Marquis of Hamilton this species interbreeds with *Cervus elaphus* ('Field,' July 1910, p. 199).

Genus AXIS Ham. Smith.

AXIS (AXIS) AXIS Erxl. (The Chital or Spotted Deer.)

(Text-fig. 132, A-E.)

Hodgson says that the preorbital glands are large and very movable, the pedal glands large and present only in the hind feet, and that the metatarsal gland is posterior and external. This is perfectly correct, according to my observations.

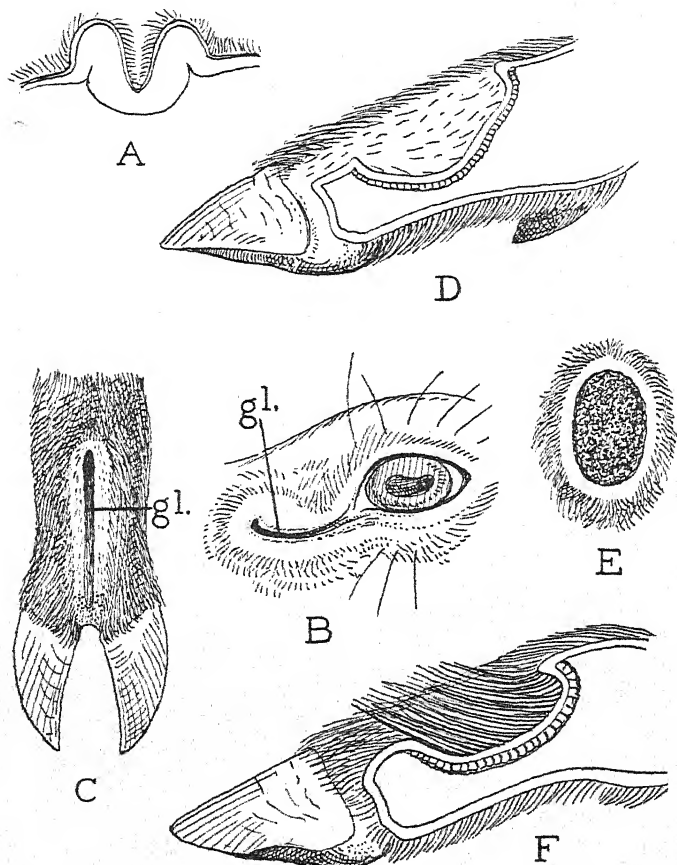
In an old male that died in the Gardens, the infolding of the preorbital gland was decidedly shallower relatively to the size of the animal than in *C. maral*, or *C. elaphus*, or *C. eldi*, and the line of the orifice, when closed, was nearly parallel to that of the long axis of the aperture of the eye and lightly concave upwards. The pocket was lined with hair of the same colour as that of the face. By squeezing, the gland could be made to yield drops of pale moisture with a faint but decided musky smell.

The metatarsal gland was represented by a horny, hairless, blackish oval patch of skin, exactly like the wart of a Zebra or Wild Donkey and surrounded by a narrow rim of pale naked skin. This patch was entirely concealed by the long hairs growing immediately round it, recalling in this respect the metatarsal gland of the Impala (*Æpyceros*).

On the front feet there was only a very shallow depression on the anterior surface of the pastern; but on the hind feet the pedal gland was well developed and represented by a long and deep depression starting at the top of the pastern and extending almost to the hoofs. At its deepest part the wall of the depression almost reached the skin of the posterior surface of the pastern. From this point it gradually shallowed above and below. Its upper edge reached the summit of the pastern, but its lower edge was sunk some distance below and above the proximal portion of the hoof, where it was continued into the interungual tie, which extended backwards from near the middle of the hoof to the heels, equalling in depth the corresponding web or tie of *Cervus maral* and *elaphus*. As in those species this tie was naked, the hairs beginning just between the heels and being continued up the back of the pastern. From the above-given description it may be inferred that the skin forming the lower rim of the inter-

digital depression is separated by a considerable space from the skin of the inferior part of the back of the pastern above the heels and that the interdigital depression, instead of communicating freely with the space between the hoofs, is to a great extent shut

Text-fig. 132.



- A. Transverse section of preorbital gland of *Axis* (*Axis*) *axis*.  
 B. Part of the face of the same showing eye and gland (*gl.*).  
 C. Anterior aspect of hind foot of same: *gl.*, slit-like orifice of gland.  
 D. Median vertical section of the hind foot of the same.  
 E. Metatarsal gland of the same with the hairs pulled aside to show naked skin.  
 F. Median vertical section of hind foot of *Axis* (*Hyalaphus*) *porcinus*.

off from it by the deep interungual tie. The walls of the depression were scantily clothed with quite short hairs stuck

together and stained with brownish secretion, and the layer of secreting cells was restricted to the walls of the interdigital depression and were much more highly developed than in *Cervus maral*.

AXIS (HYELAPHUS) PORCINUS Zimm. (The Hog-Deer.)

(Text-fig. 132, F.)

According to Hodgson, the Hog-Deer agrees with the Axis in the development and structure of its cutaneous glands, both species being referred to the genus *Axis*.

In a general way, this was true of the one example, an adult female, which I examined in a fresh state. The invagination of the preorbital gland was, however, shallower than in the male Axis. The pedal gland differed, too, in one interesting particular. Its walls were covered with a growth of long hairs projecting forwards from the orifice of the depression exactly as in the Bubaline Antelopes. These hairs were clogged basally and stained yellow by a waxy secretion with a pungent but indescribable smell. Moreover, the interungual skin of the hind foot was hairy; of the front foot it was naked, recalling what occurs in the Muntjac. The naked metatarsal patch was overlapped by the long marginal hairs as in *A. axis*.

I have seen hybrids between the Chital and the Hog-Deer in the possession of Sir Claud Alexander, by whom they were bred.

Genus DAMA Frisch.

DAMA DAMA Linn. (The Fallow-Deer.)

(Text-fig. 133.)

The structure of the feet and of the pedal glands of this Deer have been described accurately by Max Tempel. The material I have examined were a fawn about 24 hours old received from Mr. R. E. Holding, some hind feet purchased in a shop in London, and preparations of the feet in the Museum of the Royal College of Surgeons.

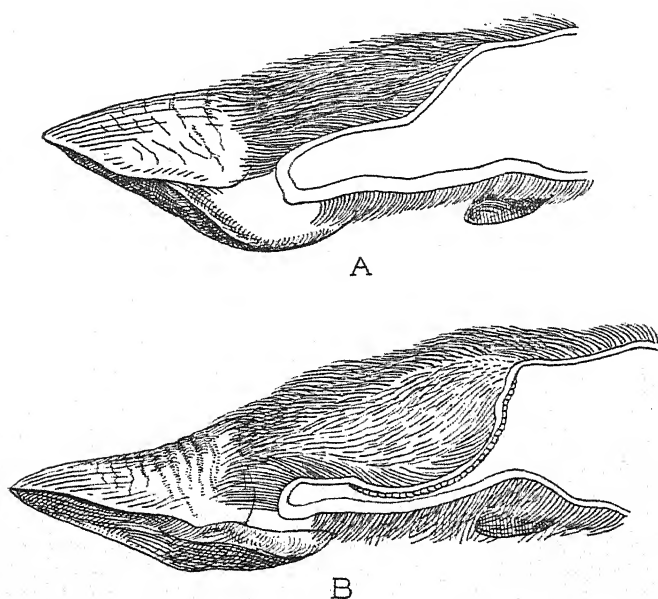
In the fawn the preorbital gland consisted of a small but very distinct pit of naked skin. This pit was considerably deeper relatively than in the much older young example of *Cervus (Rucervus) duvauceli*, but was shallower than in the fawn of *Cervulus muntjac*.

The area of the metatarsal gland was quite covered with long white close-set hair; but the gland showed no signs of activity.

The cleft of the pedal gland of the hind foot was as long as in *Axis axis* or *A. porcinus*; but the cleft itself was decidedly deeper, the skin of the posterior wall being almost in contact with that of the back wall of the pastern. As in *A. axis* the deepest part of the depression was at a point nearly midway between the heels and the false hoofs; above the deepest part the skin sloped

somewhat steeply upwards to the joint of the pastern, but below it the skin rose to only a very slight extent before passing into the heel-tie, with which it formed a close fold. Thus the interdigital cleft communicated quite freely with the space between the hoofs and was not shut off therefrom by any extension of the integument to form an interungual tie or web. The hoofs were united only at the heels; but by way of compensation for this shallow junctional area the heel-tie was very thick and horny. It was naked behind. The whole of the interdigital cleft was thickly

Text-fig. 133.

*Dama dama.*

- A. Median vertical section of front foot, from specimen in the Museum of the Royal College of Surgeons.  
 B. Median vertical section of hind foot.

clothed with hairs, growing for the most part downwards and grey or white in colour, but stained a deep yellow and stuck together basally with secretion. Inferiorly these hairs spread over the lower rim of the orifice formed by the closely folded skin above the heel-tie. The hair along the back of the pastern spread for a short distance between the heels, and the secreting cells of the gland were restricted to the walls of the interdigital cleft.

In the Museum of the Royal College of Surgeons there are preparations of the feet of this Deer. The hind foot agrees with

the one above described, and the front foot shows a very deep cleft similar to that on the hind foot but shallower, the web of the heel-tie being much less closely folded.

Although, in the opinion of some authors, *Dama* is merely a sub-genus of *Cervus*, the structure of the feet shows that it must rank as quite a distinct genus from all Elaphine Deer to which it is commonly supposed to be nearly allied. The only Deer, so far as my knowledge extends, which have the hind feet so deeply cleft are the Muntjacs (*Cervulus*) and the Chinese Water-Deer (*Hydropotes*).

I am not aware that the Fallow-Deer ever interbreeds with the Red Deer.

#### Genus CERVULUS Blainv.

CERVULUS MUNTJAC Zimm. (The Common Indian Muntjac.)  
(Text-fig. 134.)

According to Ogilby, this species has very large movable pre-orbital glands, two large movable supraorbital glands at the base of the horns, and large pedal glands. Hodgson confirms what Ogilby says about the preorbital and supraorbital glands, and adds that the pedal glands are confined to the hind feet and that the metatarsal gland is absent.

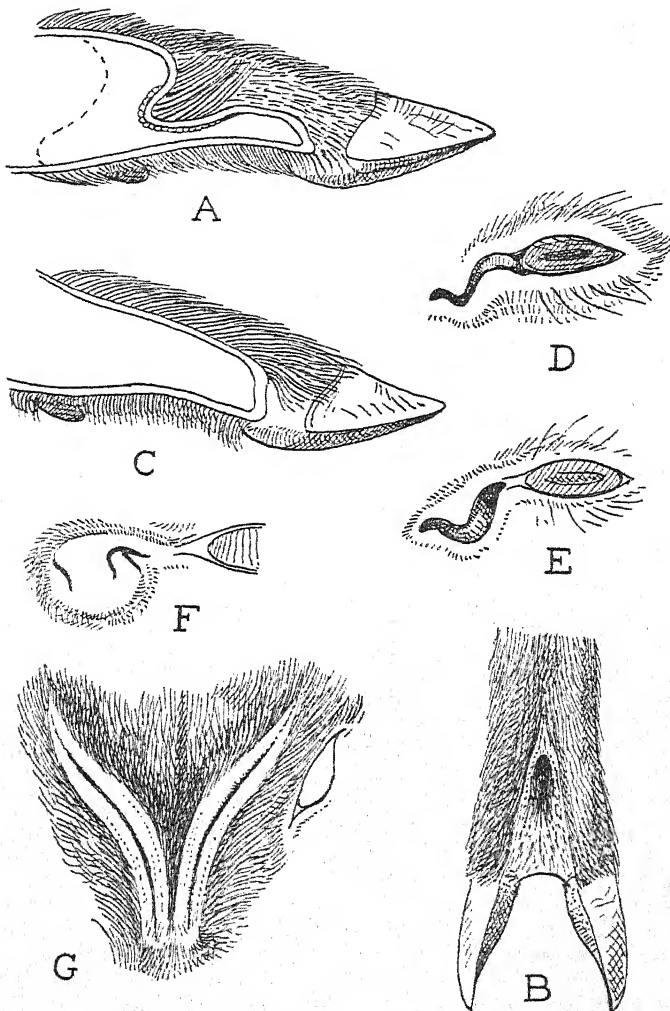
My own observations upon a specimen six days old that died in the Gardens, agreed precisely with those of Hodgson. The frontal gland was represented by two anteriorly converging strips of skin covered with very short hair, and shallowly grooved or rather longitudinally depressed along the middle line. This area of skin was in no sense thickened, and in section showed no macroscopic indication of being specially glandular. This was probably attributable to the immaturity of the specimen, for in living adult examples of this species now living in the Gardens this gland appears as a long crease with thickened upstanding edges, and, be it noted, it is much better developed in the male than in the female.

The preorbital gland when closed has the form in the adult of a crescentic slit with the concavity directed upwards. The posterior extremity of the slit, however, curves back towards the shallow groove running forwards from the eye, and its opposite extremity curves slightly the other way, giving in reality a slightly sigmoid curve to the slit. The two ends of the slit are deeper than its median portion, and when the gland was everted in the young individual its area was seen to be subcircular and marked with an anterior and posterior groove representing the deeper parts of the slit.

There was no trace of tarsal or metatarsal glands or tufts of hair; and the pedal glands were present only on the hind feet, the front of the pastern bearing a deep triangular cleft when the hoofs were separated. The skin of the back of the pastern reached the heels, and was folded somewhat closely back upon

itself, though not quite so closely as in *Dama*. The anterior skin of this fold or web formed the posterior wall of the interdigital

Text-fig. 134.



*Cerulus muntjac.*

- A. Median vertical section of hind foot of specimen six days old.
- B. Anterior aspect of hind foot of the same.
- C. Median vertical section of front foot of the same.
- D, E, F. Preorbital gland, in three stages of distension, of the same.
- G. Frontal glandular areas of the same.



cleft, the upper portion of which was depressed to form a shallow pocket with a narrow elongated orifice, whence long hairs, stuck together with secretion, projected. This pocket was the glandular area of the cleft. The sides of the cleft were covered with hair, as also was the interdigital web.

On the front foot the skin of the anterior surface of the pastern formed a very slight and gradual slope between the digits until it reached a point on a level with the heels, whence it receded somewhat abruptly, forming a moderately deep interungual web, which met the skin of the back of the pastern at right angles, constituting the heel-tie. In this foot the heel-tie and interungual web were smooth and not hairy as in the hind foot.

In a young male of about a year old examined since the one just mentioned was described, I found the glands similarly but better developed. For instance, the dark glandular layer of the pedal glands was much thicker, and the white hairs of the depression were stained a rich grass-green colour by the secretion, the smell of which might be described as "musteline," being decidedly unpleasant and reminding me of the scent of a Skunk (*Mephitis*). When the frontal gland was excised and squeezed, minute drops of clear fluid appeared on the skin. This had quite a pleasant odour, very like that of a living Civet (*Viverra civetta*) or of the waxy substance cobblers call "heel-ball."

CERVULUS REEVESI Ogilby. (Reeves' Muntjac.)

(Text-fig. 135, E.)

I had an opportunity of examining the glands on a fresh nearly adult female specimen of this species sent to the Gardens by Mr. W. Jamrach for determination. The frontal glands were not nearly so well developed as in *C. muntjac*: in the latter the nearly naked areas of skin converge and meet on the summit of the nose; but in the specimen of *C. reevesi* examined they were considerably shorter, subparallel, and separated throughout their extent by a normally hairy area of skin.

The preorbital glands were of substantially the same structure in the two. The secretion was white and adhesive, with a strong smell of cream-cheese.

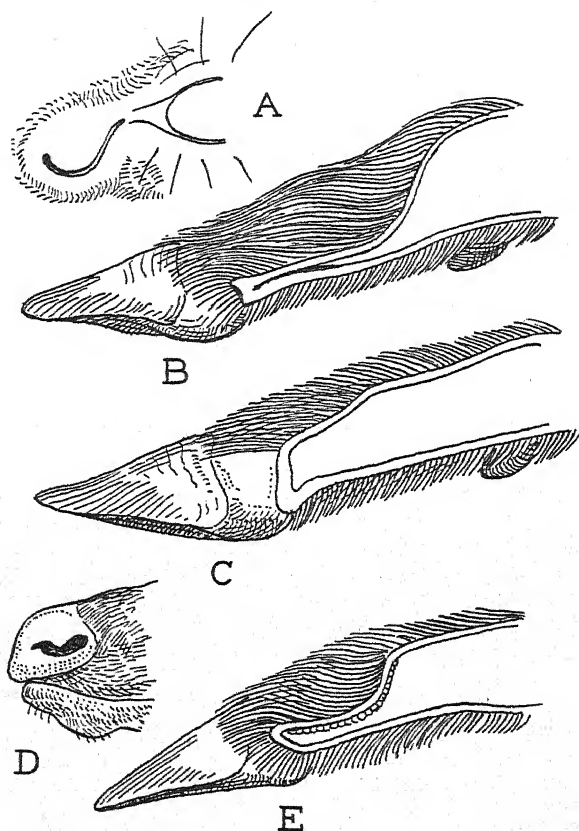
The interdigital cleft of the hind foot had no differentiated glandular pocket in its upper half, but was evenly deep throughout its length, very closely resembling that of *Dama dama*, the interdigital web consisting of a close fold of skin running along the back of the lower half of the pastern and tying the heels together where the fold began. This heel-tie and the walls of the cleft were covered with hairs, and long hairs projected forwards and downwards from its deeper portion, exactly as in the Hog-Deer (*Axis porcinus*).

Genus *ELAPHODUS* M.-Edw.*ELAPHODUS CEPHALOPHUS* or *MICHIANUS*.

(The Chinese Tufted Muntjac.) (Text-fig. 135, A-D.)

In his memoir on the anatomy of *E. michianus*, Garrod does not mention the pedal glands. He records, however, the absence

Text-fig. 135.



- A. Orifice of preorbital gland and part of the eye of *Elaphodus michianus*.  
 B. Median vertical section of hind foot of the same.  
 C. Do. of front foot of the same.  
 D. Rhinarium.  
 E. Median vertical section of hind foot of *Cervulus reevesi*.

of frontal glands and the presence of preorbital glands in both sexes\*.

\* P. Z. S. 1876, p. 757.

I am indebted to Mr. Edward Gerrard for the opportunity of examining a dry skin of a female of one of these Deer, probably referable to the Ningpo subspecies *E. cephalophus michianus*. There was no trace of frontal gland.

The preorbital glands differed in no respects from those of *Cervulus*, consisting of a subcircular area of short-haired integument with a subcrescentic crease deeper at the two ends than in the centre. The pedal gland of the hind foot resembled that of *C. reevesi*, except that the cleft was relatively longer. On the front foot there was no gland and only a shallow depression, the interungual web being moderately deep, owing to the anterior and posterior skins of the pastern being considerably separated in the middle line. The heel-tie and interungual web were quite naked. The false hoofs were of comparatively large size and the hoofs were shorter than in *C. reevesi*.

There were two pairs of teats as in other Deer. The absence of the frontal glands and the presence of well-developed false hoofs show that *Elaphodus* is a less specialised type than *Cervulus muntjac* or *reevesi*. False hoofs, however, are by no means always absent in specimens in the Gardens referred to *C. muntjac*.

#### Genus HYDROPOTES Swinh. (=HYDRELAPHUS Lydd.).

##### HYDROPOTES INERMIS Swinh.

##### (The Chinese Water-Deer.)

I have seen no example of *Hydropotes* (= *Hydrelaphus* Lydd.), but, according to Garrod (P. Z. S. 1877, p. 780), the preorbital gland was present, but quite small, in a newly-born specimen of *H. inermis*, and the metatarsal gland was absent. Of the pedal glands this author wrote:—"In the fore-limb the interdigital skin is inflected but slightly, and there is no special gland differentiated, although the surface of the skin is apparently studded with minute gland-openings. In the hind-limb the interdigital skin forms a deep pocket which almost completely separates the toes, except that they are joined by a thin transverse skin-fold along their posterior edges. The included skin is studded with small glands." I infer from this description that the posterior pedal gland resembles that of *Cervulus* or *Dama* and is quite unlike the corresponding gland of *Capreolus*, the genus near which Sir Victor Brooke placed *Hydropotes* on account of the structure of its lateral metacarpals and vomer. Since W. A. Forbes came to the same conclusion touching the affinities of these two genera judging from their visceral anatomy (P. Z. S. 1882, p. 637), there is no reason to doubt the correctness of Sir V. Brooke's view. All the more interesting, therefore, is it to find the difference in the pedal glands above alluded to; because *Hydropotes* is the only member of the Telemetacarpal Deer yet recorded as having the interdigital glandular cleft communicating

freely with the interungual space as in *Dama* and *Cervulus*, this type of gland being, in my opinion, as is explained below, the most primitive type in the Ruminants.

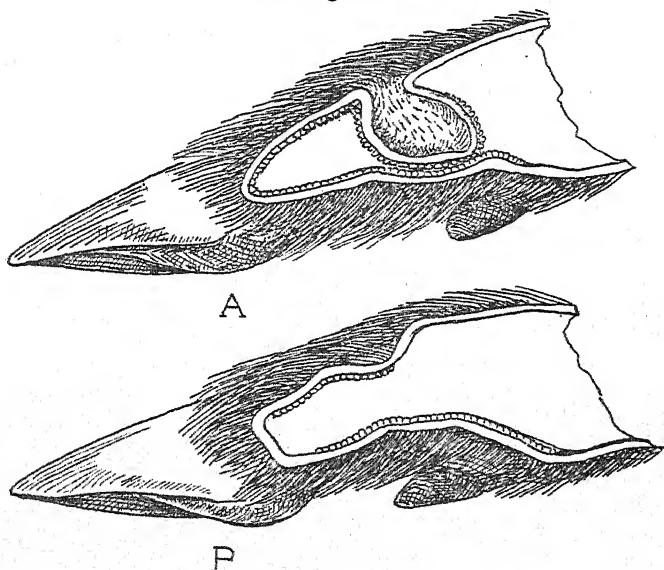
Genus *CAPREOLUS* Frisch.

*CAPREOLUS CAPREOLUS* Linn. (The Common Roe.)

(Text-fig. 136.)

According to Ogilby, this species has no preorbital glands, but large interdigital glands; and since he described the pedal glands both of *Cervus elaphus* and of *C. capreolus* as "*fossæ interdigitales magnæ*," it might be inferred that they have the same structure

Text-fig. 136.



*Capreolus capreolus*.

A. Median vertical section of hind foot. | B. Median vertical section of front foot.

in the two species. This inference, however, is as little in accord with the facts as the statement that the pedal glands of *Capreolus* are very like those of *Hydropotes* \*. Max Tempel accurately figured and described the glandular structures both on the front and hind feet of *Capreolus*.

The only material of this species which I have been able to examine was some limbs of freshly killed specimens kindly

\* Lydekker, 'Deer of all Lands,' p. 223.

procured for me by Dr. Plimmer, F.R.S., Pathologist to the Society, and by Mr. R. E. Holding, and a face-skin for which I was also indebted to the latter gentleman. Mr. Lydekker describes the face-gland of *Capreolus* as "almost obsolete." I could find no trace of it on the face-skin that I examined.

The metatarsal gland was represented by a thick pad of hairs, the bases of which exhibited blackish secretion derived from the thickened skin beneath. I could detect no distinct smell in connection with this gland.

The pedal gland of the hind foot was represented externally by a smallish orifice opening on the front of the pastern high above the hoofs. This constricted orifice led into a capacious sac extending as far back as the posterior skin of the pastern and also to a certain distance upwards, its upper extremity reaching as far as the false hoofs. The walls of the sac were scantily clothed with long pale hairs all stuck together with thick yellow secretion smelling like cheese. The dark brown gelatinous-looking glandular layer enveloped not only the sac itself but the skin of the front of the pastern below it and the skin of its posterior side up as far as the false hoofs. The hair between the hoofs was all matted with secretion. Below the orifice of the glandular pouch the skin of the middle line of the pastern was only slightly depressed; the anterior and posterior walls of the interungual web were moderately widely separated and in no sense closely folded as in *Cervulus* or *Dama*. This web was, however, uniformly and thickly covered, both above, below, and between the heels, with long hairs.

On the front leg the glandular sac was represented by a very shallow depression, but the skin of the pastern below this down to the hoofs and of the back of the pastern from the heels up to the false hoofs was lined with a dark secreting layer. This layer did not, however, extend up the interungual web, which was deeper than that of the hind foot but similarly hairy. The hairs both on the front and the back of the pastern were stuck together basally with blackish sticky secretion smelling of mouse urine.

#### Genus *ALCE* Frisch.

*ALCE ALCES* Linn. (The Moose.)

(Text-fig. 137.)

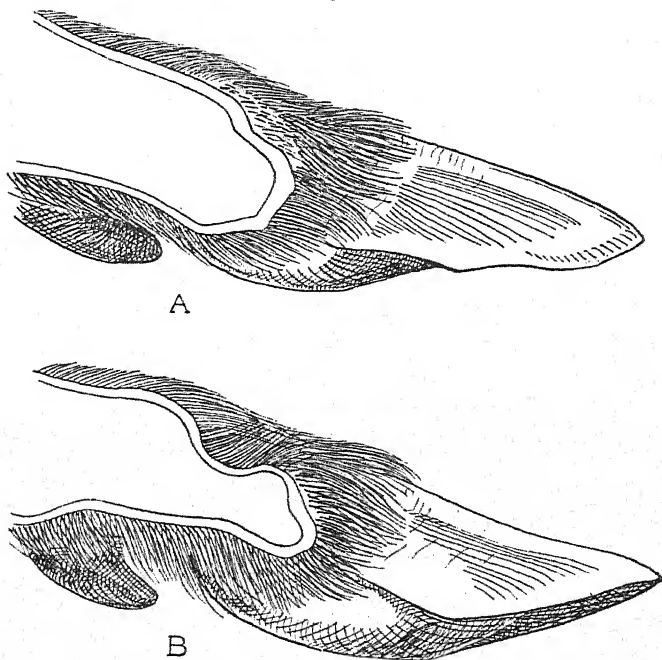
According to Ogilby, this species has large preorbital and pedal glands. Subsequent authors have also recorded the presence of preorbital, tarsal, and metatarsal glands, the latter, according to Nitsche (Zool. Anz. xiv. p. 181, 1891), being represented by a naked area of skin overlapped by a marginal fringe. Max Tempel accurately described the structure of the feet and the microscopic structure of the glandular pocket of the posterior foot.

I have nothing new to add on these points, the only material of the genus I have been able to procure for examination being

two feet which, from certain differences in their structure, I judge to be those of front and hind legs. The former I received from Mr. R. E. Holding, the latter from Messrs. Rowland Ward, Ltd.

On the one judged to be the hind foot the interdigital pocket found in *Capreolus* and *Rangifer* was represented by a distinct but shallow depression, with hairs paler than those of the surrounding skin projecting from it. A little below this the integument dipped obliquely backwards and downwards towards the heels to meet that of the posterior side of the pastern, which extended for some distance between the heels but was not markedly thickened to form a strong heel-tie. The entire interungual-area and heel-tie were covered with long hairs, there being only a small less thickly haired area a little below the glandular depression.

Text-fig. 137.



*Alce alces.*

- A. Median vertical section of front foot (dried).
- B. The same of hind foot (dried).

On the front leg there was scarcely a trace of the glandular pocket seen on the other, but the slightly depressed skin along the middle line of the front of the pastern towards the hoofs was scantily hairy, this area being of much greater extent than on the foot previously described. Moreover, the interungual web

was much thicker and deeper, the two halves of the hoof of the front foot being evidently much more strongly united than those of the hind foot. As in the latter, the whole interungual tie was thickly covered with long hairs, this hairy clothing constituting a marked difference between the feet of the Moose and those of the Red Deer group, and showing equally marked similarity between the Moose, Roebuck, Reindeer, and typical American Deer.

Genus RANGIFER Frisch.

RANGIFER TARANDUS Linn. (The Reindeer.)

(Text-fig. 138.)

According to Ogilby, this Deer has large preorbital and small pedal glands. Max Tempel shows that there is a well-developed glandular pocket on the hind foot, but none on the front foot. My own observations are completely in accord with this.

The only material of this species I have been able to examine was the fore and hind feet of the Caribou (*R. tarandus caribou*) lent to me by Mr. Gerrard, and the fore foot of a second example received from Messrs. Rowland Ward, Ltd.

The tarsal gland consisted of a large area of thickened skin covered with a mat of long coarse white hairs without underwool, the bases of the hairs being clogged with colourless scurfy secretion.

The pedal gland opened by a large orifice on the front of the pastern some distance above the proximal edge of the hoof. The orifice led into a deep subcylindrical pocket, the deeper end of which extended obliquely backwards and upwards in the direction of the false hoofs. The cavity of this sac was filled with long hairs, all directed towards the orifice and stained yellow, and a well-marked dark-coloured secreting layer enveloped the walls of the sac within the pastern. The interungual web was very short, and was situated some distance from the heels towards the proximal end of the hoof in front, forming in section a semi-elliptical figure. Like the back and the front of the pastern, it was thickly covered throughout with long hair.

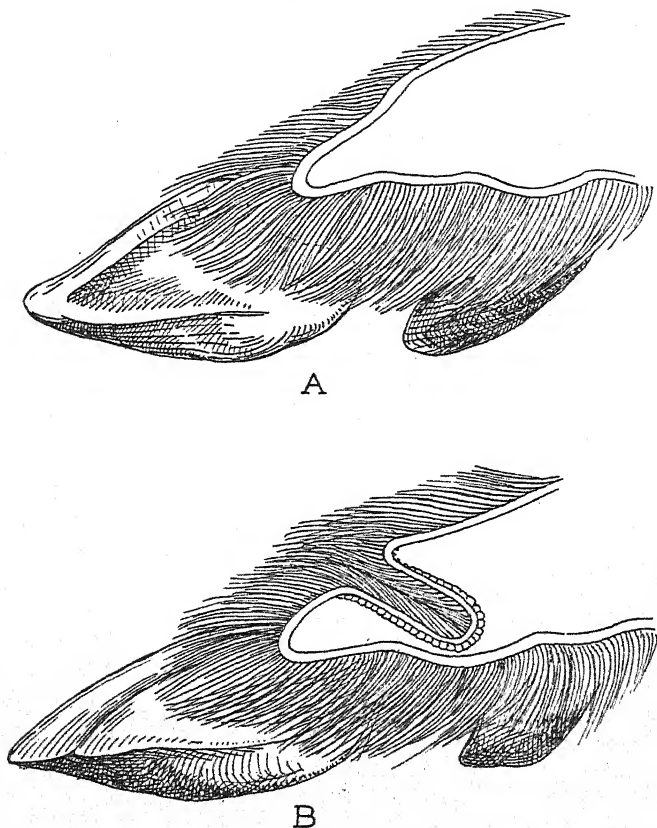
The front foot was, in a general way, like the hind foot, but had no trace of the glandular pocket, and the interungual web was even less extensive and still further removed from the heels.

The resemblances between the glands of the feet of the Reindeer and those of the Roe (*Capreolus*) or Brocket (*Mazama*) are unmistakable, and are quite in accord with Sir Victor Brooke's view of the relationship between these Deer.

Writing of the foot of the Reindeer, Flower and Lydekker remark:—"The cleft between the two main hoofs is very deep, so that these hoofs can be spread out as the animal traverses the snow-clad regions in which it dwells" ('Mammalia,' p. 325, 1891). This expression, although true in a sense, by no means conveys an accurate impression of the cause of the potential expansion of

the hoofs of this species, nor does it suggest the difference between the distensibility of the hoofs in the Reindeer and those of the Red Deer for example.

Text-fig. 138.



*Rangifer tarandus.*

A. Median vertical section of front foot (dried).

B. The same of hind foot (dried).

The peculiarity of the foot of the Reindeer consists in this:—The integumental web joining the two hoofs together passes straight forwards some distance above the heels and terminates behind and nearly on a level with the upper posterior margin of the nail. From this arrangement it results that whereas the superior and proximal portions of the hoof are capable of comparatively little distension, the heels can be widely separated, giving to the hoof a wide plantar area which is increased by the long false hoofs. It is only when the hoofs are thus distended



that the plantar surface, or sole, of each is applied flat to the ground, on account of the much greater size of the external as compared with the internal lamina of the nail.

Genus DORCELAPHUS Gloger.

DORCELAPHUS (or CARIACUS) AMERICANUS Erxl.

(The Virginian Deer.) (Text-fig. 140, C, p. 965.)

I have had no dead example of this species for examination, but in the collection of the Royal College of Surgeons there are mounted specimens of the fore and hind feet showing the pedal glands. The glands on the hind foot resemble in a general way both in position and development those of the Roebuck (*Capreolus*), except that the orifice is relatively larger and less constricted. As in the other Telemetacarpal Deer that I have seen, the interungual integument is covered with longish hairs, continuous in front and behind with those of the anterior and posterior sides of the pastern respectively.

The front feet are similarly constructed, and have a large pocket-like gland resembling that of the hind feet but smaller. This is the only species of Deer known to me which has a large pedal gland on the fore foot.

The presence of preorbital, tarsal, and metatarsal glands in this and allied species has been recorded by other writers, and they are all apparent upon a living specimen in the Gardens, from Venezuela, which I identify as *D. americanus savannarum*.

Genus MAZAMA Raf.

MAZAMA NEMORIVAGUS F. Cuv. (The Wood-Brocket.)

(Text-fig. 139.)

I have examined one adult female of this species.

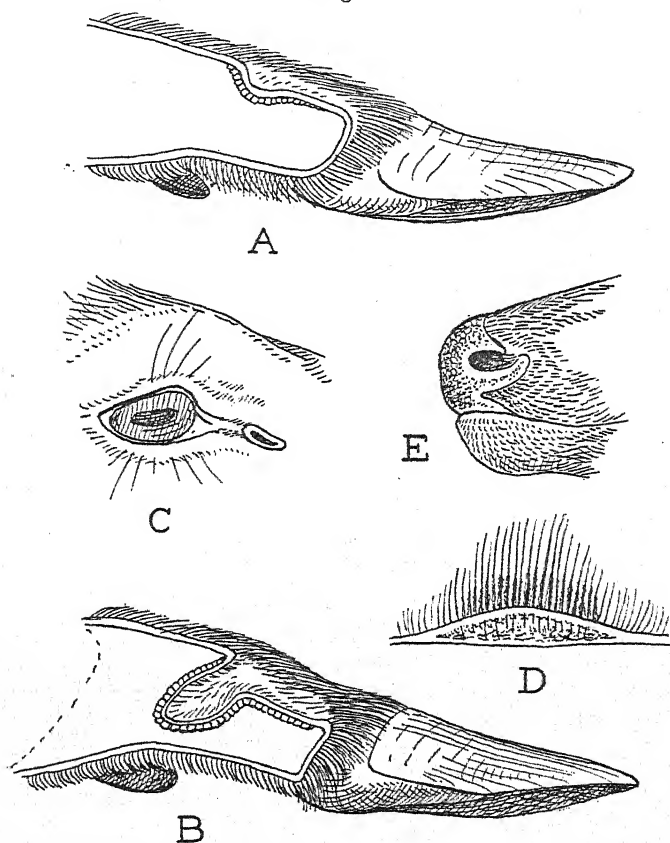
The preorbital gland was a small shallow infolding, linear when closed and subelliptical when spread, resembling that of an eighteen months old *Cervus sika*.

The hock- or tarsal gland was marked externally by a small tuft of whitish or ashy-grey hairs arranged in a whorl and with their bases encrusted with dark brown secretion, the underlying skin being thick in section, with the roots of the hairs penetrating deeply into it. There was no metatarsal gland.

The pedal gland was well developed upon the hind foot. The front of the pastern was marked by a shallow triangular depression, at the summit of which was the orifice of a cylindrical sac resembling that of the Reindeer (*Rangifer*), the deep end of the pocket reaching nearly to the false hoofs. The walls of the pocket were sparsely lined with hairs covered with secretion which stained black the longer hairs of the depression below the orifice of the gland. The secreting layer of cells enveloped the pocket and extended along the skin forming the posterior wall of

the depression down to the point where it passed into the interungual web. This was deep and projected straight backwards from a point about on a level with the middle of the proximal edge of the nail nearly to the posterior part of the heels, meeting at right angles the skin of both the anterior and posterior walls of the

Text-fig. 139.

*Mazama nemorivagus* ♀.

- A. Median vertical section of front foot.
- B. The same of hind foot.
- C. Ocular region and preorbital gland.
- D. Section of tarsal gland.
- E. Rhinarium.

pastern which were widely separated. The interungual web was uniformly covered with longish hairs barely overlapping the proximal edge of the nail. The hoofs were long and pointed.

The front hoof was constructed almost exactly like the hind,

except that the pocket was represented by a very shallow depression, and the area of the pastern below this was scarcely depressed. The secreting layer of cells lined the integument in exactly the same way.

I believe this species to have been correctly determined; yet, according to Fitzinger, *M. nemorivagus* has no tarsal gland, and was consequently made the type of that author's genus *Doryceros*.

MAZAMA BRICENII Thos. (Briceni's Brocket.)

(Text-fig. 140, A, B.)

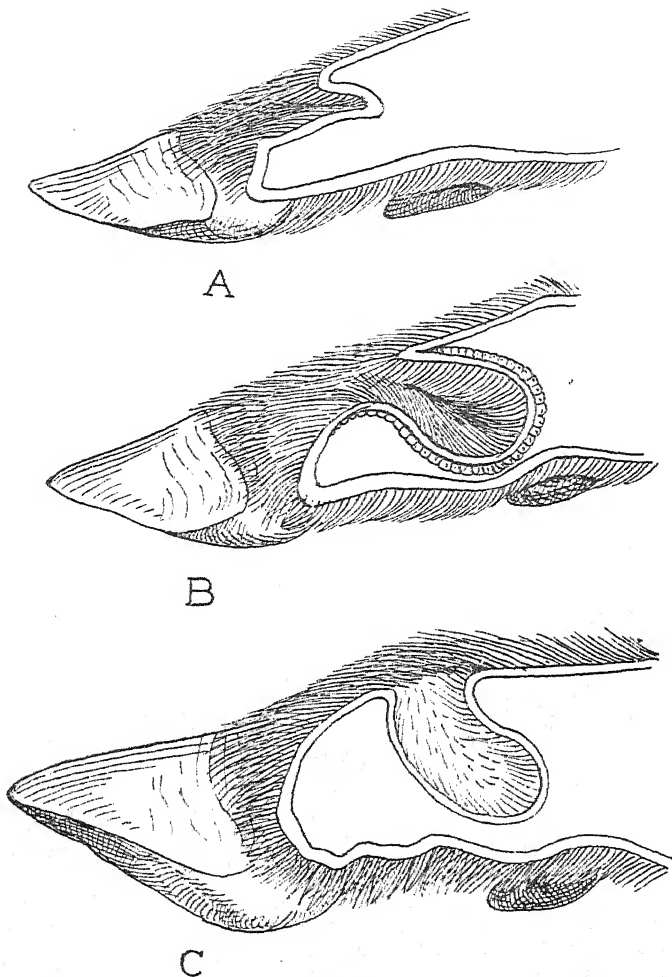
A single adult female example from Venezuela. The preorbital gland resembled that of *M. nemorivagus*. Superficial examination of the hock showed no trace of the tarsal gland, but when the hairs over the appropriate spot were rubbed aside they were seen to have darker bases than elsewhere on the leg and the underlying integument was thickened as in *M. nemorivagus* although to a much less degree. On a dried skin these glands would probably have been wholly overlooked, since they were not marked by any tuft of hairs thicker or coarser than those surrounding the area.

The feet were rather differently constructed from those of *M. nemorivagus*, the hoofs being very much shorter, the interdigital cleft on the front of the pastern deeper, and the interungual web shallower. On the hind foot the glandular pocket was capacious and deep, extending backwards and upwards and touching the skin of the posterior side of the pastern just below the false hoofs. It was nearly elliptical in section, the lumen of the sac being larger than the orifice. Just below the orifice the integument formed an arched curve down to the strong heel-tie. The walls of the pouch were thickly and uniformly covered with long hairs projecting towards the orifice; and the walls of the interdigital cleft and the heel-tie were also covered uniformly with hairs. An olive-brown glandular secreting layer enveloped the pocket and extended inferiorly nearly to the heel-tie. On the front foot the pocket, although small as compared with that of the hind foot, was better marked than in any species of Deer I have examined with the exception of *Dorcelaphus americanus*, consisting of a very definite hair-lined invagination. Below the orifice the skin of the anterior surface of the pastern passed towards the hoofs in a direction parallel to that of the posterior side of the pastern, then descended obliquely downwards and backwards to the heel-tie, which for a short distance was hairless, thus differing from the corresponding area in the hind foot, and recalling the similar difference between the two feet of the Muntjacs (*Cervulus*).

Since pedal glands essentially similar in structure and position are found in such widely-divergent genera of Telemetacarpal Deer as *Rangifer*, *Capreolus*, *Dorcelaphus*, and *Mazama*, it may be inferred that they are present at least upon the hind feet in the

other Deer of this group, the genus *Pudu* alone constituting an exception.

Text-fig. 140.



A. Median vertical section of front foot of *Mazama bricenii* ♀.

B. Do. of hind foot of the same.

C. Do. of hind foot of *Dorcelaphus americanus* from specimen in the Museum of the Royal College of Surgeons.

I have had no opportunity of examining the feet or fresh skins of any examples of the following types of Telemetacarpal Deer. The principal external features of the glands will be found described in Mr. Lydekker's monograph.

Genus *EUCERVUS* Gray.*EUCERVUS HEMIONUS* Raf.

(The Mule Deer.)

Nothing, so far as I am aware, is known of the structure of the feet; but the preorbital, tarsal, and metatarsal glands are present, the metatarsal gland being unique in its length, since it extends at least halfway down the cannon-bone towards the fetlock. This character I have used as a generic feature to distinguish *Eucervus* from *Dorcilaphus* (p. 971).

Genus *BLASTOCERUS* Sund.*BLASTOCERUS DICHOTOMUS* Ill. (= *PALUDOSUS*).

(The Marsh-Deer.)

The preorbital and tarsal glands are present and the metatarsal gland absent, according to Mr. Lydekker. In this last-mentioned character the Marsh-Deer resembles *Mazama*.

*BLASTOCERUS BEZOARTICUS* Linn. (= *CAMPESTRIS*).

(The Pampas Deer.)

This species appears to resemble the foregoing in the nature of its glands.

The difference in the antlers suggests that this Deer should rank as a genus (or subgenus) distinct from *B. dichotomus*.

Genus *HIPPOCAMELUS* Leuck.*HIPPOCAMELUS BISULCUS* Mol.

(The Chilian Guemal.)

Under the name *Xenelaphus*, Mr. Lydekker admits this and its ally *H. antisiensis* as a subgenus on account of the simply forked antlers, the coarse brittle hair, and the absence of the metatarsal gland. The latter, however, is also wanting in *Blastocerus* and *Mazama*, leaving the subgeneric status dependent on the character of the coat and antlers. This author also remarks that the simple form of the antlers is seemingly due to degradation and cannot therefore be regarded as an ancestral type, because the absence of spots in the fawn and the suppression of the metatarsal gland are obviously specialised features. Yet there is no commoner morphological phenomenon than the association of primitive with specialised features in a species. Moreover, the antlers of *Hippocamelus* and *Mazama* may be due to simplification from a much more complex type and yet be "ancestral" in the sense that their characters result from the retention to maturity of an early growth-stage.

Genus *PUDU* Gray.*PUDU PUDU* Mol. (The Chilean *Pudu*.)

I have had no opportunity of examining any material of this genus beyond the dried skins in the collection of the British Museum. According to Flower (P.Z.S. 1875, p. 160), the preorbital gland in *P. pudu* "is a distinct involution of thickened integument . . . with an aperture half an inch in length," and the pedal glands are not represented by distinct pouches, "but the skin in the depression between the toes on the dorsal surface of all the feet is bare and evidently has a free sebaceous secretion," representing, in the author's opinion, "the most rudimentary or earliest stage of an interdigital gland" (see p. 978). So far as it is possible to form an opinion from this description, it may be inferred that the interdigital depression in this aberrant genus closely, and it must be admitted surprisingly, resembles that of such species as *Cervus elaphus* or *C. eldi*.

Lydekker says both tarsal and metatarsal glands are absent ('Deer of all Lands,' p. 307).

*The Classification of the Cervidae.*

From the account just given of the cutaneous glands of the Deer, it may be inferred that I think Sir Victor Brooke's classification of this family is correct, and Mr. Gordon Cameron's incorrect in the particulars in which it differs from Brooke's. It is important to refer to this matter, because in Mr. Lydekker's volume on Deer, to which recent authors not unnaturally refer as a standard work, Brooke's classification is set aside in favour of Cameron's, which gives primary importance to the antlers as a basis for the major divisions of the Cervidæ\*.

Briefly stated, Mr. Cameron classifies the Deer into four groups:—(1) *Rangifer*, with antlers in both sexes; (2) *Alce*, with antlers rising laterally on the sides of the skull; (3) mostly American Deer of small or medium size, termed collectively *Cariacus*, with which are associated *Capreolus* and *Elaphurus*, a section characterised by "forked" antlers without a brow-tine; (4) all the Deer of the Old World, except those mentioned above, including *Cervus* and *Cervulus*, which are distinguished by antlers consisting of a "beam," usually itself branched with a basal "brow-tine." These third and fourth sections are, however, derivable from a common stock, from which *Rangifer* and *Alce* are excluded as "strangers to one another and to all other groups from the time when antlers first distinguished the family" (The 'Field,' 1892, p. 703).

*Rangifer* is considered to be a primitive type on account of the occurrence of antlers in both sexes and their early appearance in

\* The 'Field,' 1892, pp. 625, 703, 741, 860. In the 'Field' for 1910, pp. 154, 215 (July), this classification was upheld by Mr. Cameron in opposition to the views advocated in this paper and summarised in the 'Field,' 1910, p. 97 (July).

the young. This assumption I believe to be false. If true, we should expect to find antlers of a primitive type in *Rangifer*. This, however, is not claimed, Mr. Cameron describing those of the Caribou "as the most specialised of existing antlers." Yet their fundamental resemblance to the antlers of the Deer, in which these weapons are well developed, is clear enough; and this fact is difficult to explain in conjunction with Mr. Cameron's double claim that the antlers of *Rangifer* are highly specialised and that the genus has followed a line of its own in evolution, independent of all existing species. The characters of *Rangifer* are, in my opinion, much more easily interpreted on the hypothesis that the genus is a specialised representative of the Doreclaphine (Cariacine) Deer.

In the case of *Alce*, the lateral direction of the antlers is admittedly a peculiarity; but it is as obviously a derivative, not a primitive, feature. As for the antlers themselves, they are, in their simple form, clearly referable to the so-called "forked type" characteristic of Mr. Cameron's third section of Deer; and *Alce*, like *Rangifer*, may be best interpreted as a specialised member of that group.

Mr. Cameron also claims some support for his view of the great antiquity of these two Deer on the ground of their wide range in space; but although it may be true, very broadly speaking, "that types which have a wide range in time have also a wide range in space," there are probably no species in the world to which this remark applies with less force than it does to those inhabiting subarctic latitudes. For it is known that in comparatively recent geological times subarctic regions formed a continuous tract of land with similar physical conditions, offering no barrier to the eastward or westward migration of the indigenous species adapted to the surroundings.

The antlers of Mr. Cameron's third group (*Cariacus*, *Capreolus*, *Elaphurus*) are derivable, using his own words, from antlers consisting of a "forked beam with equal or subequal prongs," the Neotropical Guemal (*Hippocamelus*) being cited as an illustration; while the antlers of his fourth group (*Cervus*, *Cervulus*) are derivable from an "unbranched beam with a true brow-tine."

The terminology here employed is apt to confuse the issue. It suggests a fundamental difference between the two types of antlers described, whereas, on the face of it, it appears that Mr. Cameron is describing in different words structures which are to all intents and purposes identical. An "unbranched beam with a brow-tine" and a "forked beam" are alike describable as biramous antlers consisting of an anterior and a posterior prong arising from a common base, the anterior branch of the "forked beam" corresponding to the "brow-tine" and its posterior branch to the so-called "beam." Until this suggested homology be disproved, Mr. Cameron's assumption of the fundamental diversity of the two types of antlers cannot be regarded otherwise

than as an interesting speculation; and his conclusions are open to the criticism of being based upon premises which cannot, on the evidence, be accepted as firmly established.

Looking at the antlers of an adult Red Deer, Wapiti, Barasingha, Thameng, or Japanese Deer, it seems absurd to claim that the "brow-tine" is equivalent to the so-called "beam" which constitutes the rest of the antler. It appears merely to be the lowest of the series of branches which arise from the beam and to be comparable to those that are above it. The accepted terminology of the tines bears out this interpretation. I believe, nevertheless, that the "brow-tine" and the "beam" are respectively the anterior and posterior branches of an originally subequally biramous or dichotomous antler, like that, for instance, of the Guemal (*Hippocamelus*), and that their real equivalence in the Deer above-named is obscured by the immense development and complex armature of the posterior branch. It is this growth of the posterior branch at the expense of the anterior which characterises the antlers of most of the Deer of the Old World. A marked approach to this inequality is seen in the Reindeer, but in this genus the fundamental equivalence between the two branches is more apparent. Limitations to the growth of the anterior branch are imposed probably by necessities of feeding. If the anterior branch projected beyond the muzzle, a Stag could not feed with freedom off the ground; and even if it were prolonged obliquely upwards over the face, it would be a hindrance to browsing. No such limitations exist in the case of the posterior branch.

Support for the hypothesis that the antlers of the so-called Elaphine group were originally biramous like those of the Guemal (*Hippocamelus*), and that the biramous antler was preceded in evolutionary development by an unbranched antler such as is retained in *Mazama*, is supplied by the annual growth of an individual antler. The antler first appears as an undivided bud corresponding, I conceive, to the unbranched antler of *Mazama*. This bud then gives off an anterior and a posterior branch. For a longer or a shorter time these grow with equal rapidity, forming a biramous antler which in species with the anterior branch inclined upwards, as in the Axis, Sambar, or Japanese Deer, is shaped like a short-stalked Y, resembling, in fact, the permanent antler of the adult Guemal (*Hippocamelus*).

These stages are not equally evident in all Stags. In *Cervus* itself, for example, the early appearance of the "bez"-tine makes the biramous appearance of very short duration; but in the Thameng or Panolia Deer (*C. eldi*) the anterior and posterior branches grow at the same rate until the anterior branch has reached nearly its full size. Thereafter the posterior branch rapidly surpasses it and, increasing in length, develops its supplementary tines.

If this view of the fundamental resemblance underlying the antlers of all Deer be correct, it minimises the difficulty of



classifying *Elaphurus* with the Elaphine Deer, where Brooke, in my opinion, correctly placed it. For, according to this reading of the facts, the antlers of *Elaphurus* have not passed far beyond the biramous stage, seen transitorily but quite clearly in the growing antlers of such Deer as *Rusa*, *C. (Panolia) eldi*, and others. The peculiarities of the antlers of *Elaphurus* consist in the lengthening of the basal portion, the lengthening and bifurcation of the anterior branch which concomitantly has a strong upward trend so as to clear the face, and development of the posterior branch into a long slender usually undivided tine.

I suggest this homology of the anterior and posterior branches of the antlers of *Elaphurus* with the so-called "brow-tine" and "beam" of the antlers of the Elaphine group, because this Stag has evidently been the stumbling-block in the way of the acceptance of Brooke's classification both to Mr. Cameron and Mr. Lydekker. The latter, indeed, writes strongly on the point. He says: "If antlers count for anything in classification . . . the genus [*Elaphurus*] has nothing to do with any of the living Old World Deer with the exception of the Roes, while its alliance with the American Deer seems close" ('Deer of all Lands,' p. 234). Of course, antlers count something in classification; but whether they count as much as Mr. Cameron and Mr. Lydekker believe is quite another matter. In my opinion they do not; and I think the resemblance between *Elaphurus* and the American Deer, or at all events some of them, consists in the fact that the antlers in both have been specialised to a comparatively small extent beyond the biramous stage, which was, I believe, common to all Deer after the one-pronged or mazamine stage was passed. I do not think it can be claimed that such a resemblance is strong evidence of affinity.

Adopting, then, as a basis for the classification of the Cervidæ the skeletal characters pointed out by Mr. Garrod and Sir Victor Brooke, I give the subjoined analytical key of what appear to me to be unquestionably valid genera tested by the feet and glands alone. Of course, I speak on this point with reserve as regards the American forms like *Hippocamelus*, *Blastocerus*, and *Eucervus*, which I have not seen. Very possibly there are more genera to come into his section than I have admitted. Of the Deer of the Old World I am more confident. It must be remembered, however, that the genera of this family have been established for the most part upon characters other than those forming the subject-matter of this paper, the branching and mode of growth of the antlers being the principal one. I have not in all cases made use of these characters because they are well known and have been repeatedly described.

In the preceding pages I have, without prejudice, adopted such names as *Hyelaphus*, *Rucervus*, *Panolia*, and *Pseudaxis* as connoting groups of subgeneric rank. I have, however, no confidence in the permanent admission of any of them as subgenera. In the future they will probably be granted full generic status; but this course or that of regarding them as subgenera or as synonyms

of *Axis* and *Cervus* will depend upon the views of each individual taxonomist. The point I wish to emphasise is that the characters on which they were established have not, in my opinion, so high a systematic value as those to which full generic importance is here attached. I do not, for example, think that in the future *Dama* will be set down as a subgenus of *Cervus*, whatever course may be adopted with regard to *Rucervus*, *Panolia*, or *Pseudaxis*.

- a. Distal portion of lateral metacarpals persistent, interungual integument, where known, thickly hairy. (*Telometacarpalia*). CAPREOLINÆ
- b. Naviculo-cuboid and external cuneiform bones of tarsus united; no pedal, tarsal or metatarsal glands ..... *Pudu*.
- b'. Naviculo-cuboid and external cuneiform bones of tarsus separated; pedal glands present at least on the hind feet (? in *Eucervus*, *Blastocervus*, *Hippocamelus*); tarsal or metatarsal gland, sometimes both, present.
- c. Vomer dividing the posterior narial aperture.
- d. Rhinarium large; hoofs narrower, tied together posteriorly or throughout their posterior half; pasterns not depressed behind.
- e. Metatarsal gland very long ..... *Eucervus*.
- e'. Metatarsal gland normal or absent.
- f. Metatarsal gland present; a large pocket-like pedal gland on the front as well as on the hind foot ..... *Dorcelaphus*.
- f'. Metatarsal gland absent; at most a small glandular pocket on the front feet (? in *Blastocervus* and *Hippocamelus*).
- g. Preorbital glands moderately large; antlers branched. *Blastocervus*, *Hippocamelus*
- g'. Preorbital glands small; antlers unbranched ..... *Mazama*.
- d'. No rhinarium, muzzle hairy; hoofs broad, widely separable at the heels, owing to the anterior position of the web; pedal glands on the hind feet only, and consisting, as in *Mazama*, *Dorcelaphus*, and *Capreolus*, of a deep pocket opening high up the pastern; tarsal and preorbital glands large ..... *Rangifer*.
- c'. Vomer not dividing the posterior nares.
- h. Pedal gland either a deep and long interdigital cleft or a large pouch with constricted orifice on the hind foot; rhinarium large; no tarsal gland.
- i. Pedal gland a large pouch, with constricted orifice opening high up the pastern; preorbital gland absent; metatarsal gland present ..... *Caprenius*.
- i'. Pedal gland a deep interdigital cleft, the hoofs united at the heels by a fold of integument; preorbital gland present; metatarsal gland absent ..... *Hydropotes*.
- h'. Pedal gland a comparatively small invagination situated as in *Capreolus* and *Rangifer*; rhinarium very small; tarsal and preorbital glands present; metatarsal gland small or absent ..... *Alce*.
- a'. Proximal portion of lateral metacarpals persistent or occasionally wanting. (*Plesiometacarpalia*) ..... CERVINÆ.
- k. Tarsus with naviculo-cuboid and cuneiform bones united; pedal gland a deep cleft on the hind feet; hoofs united only at the heels ..... *Cervulus*, *Elaphodus*.
- k'. Tarsus with naviculo-cuboid and cuneiform bones separated.
- l. Hoofs of hind feet united only at the heels by a close fold of skin; the gland a long and deep hair-lined interdigital cleft as in *Cervulus*; a moderately deep cleft also on the pastern of the front foot ..... *Dama*.
- l'. Hoofs of hind feet united almost throughout their basal depth by a deep interungual web; no deep cleft on pastern of front foot.
- m. Pedal gland a long and moderately deep cleft on the pastern of the hind feet; metatarsal gland naked, overlapped by marginal hairs ..... *Axis*.

- m'*. No specialised gland or deep cleft on front or hind feet; metatarsal gland overgrown with hairs, occasionally absent; interungual integument naked.
- n*. Rhinarium extending some distance beneath the nostrils, as in *Axis*; tail long.
- o*. Tail bushy; antlers with short base, short undivided anterior branch and long, stout, two-pronged posterior branch..... *Rusa*.
- o'*. Tail tufted; antlers with long base, long, usually two-pronged anterior branch, and long, slender, usually undivided posterior branch..... *Elaphurus*.
- n'*. Rhinarium extending only a short distance below the nostril; tail (except in *Pseudavis*) quite short..... *Cervus*.

### Family CAMELIDÆ.

(Text-fig. 142, A, p. 981.)

According to Ogilby, Camels and Llamas have neither preorbital, inguinal, nor interdigital glands.

I have had no opportunity of examining fresh examples of either species of *Camelus*, but, according to Max Tempel, *C. dromedarius* has specialised glands in the interdigital cleft of both the front and hind feet. In the foot of a Vicuna (*Lama vicugna*) that died in the Gardens I found the pedal glands to be as well developed as in some Cervidæ, in the sense that the integument of the interdigital cleft secreted a strong-smelling substance. The hairs on the front of the pastern passed about halfway down the walls of the cleft, leaving the deeper half quite naked. In the specimen examined this naked area was covered with brown sticky substance smelling exactly like the urine of *Mus musculus*. The depth of this cleft is due to the fact that the integument of the back of the pastern, which extends to a point halfway between the heel and the nail of the hoof, is closely folded back upon itself, forming a shallow but long interdigital web.

The peculiarity of the foot of the Llama as compared with that of the Bovidæ is the small size of the nail and the length of the sole and of the heel as compared with it. The apex and lower edges of the nail, however, extend for a short distance on to the plantar aspect of the foot.

From the remark in Flower and Lydekker's 'Mammalia' (p. 295) that there is "a broad cutaneous pad, forming the sole of the foot, on which the animal rests in walking, instead of on the hoofs," one might be led to infer that the manner of walking in the Camelidæ differs essentially from that of other Ruminant Ungulates in that the latter walk upon the nails and the former upon a cutaneous pad behind the nail. This is not the case. All the ruminant Ungulates the feet of which I have examined, with the single exception of the Klipspringer (*Oreotragus*), walk upon the cutaneous pad forming the sole and heel of the hoof, and upon more or less of the inferior edge and apex of the nail in front. The Camels form no exception to this rule, the only difference being that the small nail does not invade the area of the sole to anything like the same extent, and that the sole and

the heel are continued farther backwards. In other words, it is only a difference in the degree of development of the parts composing the distal portion of the foot.

As is well known, the plantar area of the hoof in late fetal and many, perhaps all, newly born Cervidae and Bovidae is quite soft right up to and in some cases beyond the apex of the nail. This terminal portion soon shrivels and hardens, and becomes, in most cases at all events, indistinguishable from the inferior portions of the nail, especially externally; but usually the line of demarcation between the nail and the sole can be quite easily detected, especially on the inner aspect of the hoof, showing that the sole, although hard and horny, still persists and forms with the heels the main area of support during progression. The one exception to this rule known to me is the Klipspringer, which appears to support itself entirely upon the truncated apex of the nail of the hoof, with possibly a small piece of the hardened sole wedged in the angle formed by the two sides of the nail.

The males both of *Camelus dromedarius* and of *C. bactrianus* have a pair of well-developed glands on the summit of the neck just behind the occiput. In the living animal these may be easily felt as a pair of oval or roundish lumps lying close together. The hair overlying them has no underwool. In a male of *C. dromedarius* I have seen black watery secretion running from these glands and dropping off the hairs like sweat. This was in the month of June, when the glands of a male *C. bactrianus* were quite inactive. In the latter animal the glands were active and giving off a powerful repulsive odour much earlier in the year—that is to say, in March. The smell of the secretion from the glands in the Dromedary was equally repulsive, but reminded me of no substance in particular. It stains the skin of the fingers in much the same way as walnut-juice does. The position of the glands in the Dromedary is easily seen by the post-occipital patch of black hair. I have had no opportunity of observing the gland in the female Dromedary; but in the female Bactrian Camel it is much smaller than in the male, and never apparently noticeably active as it is in the latter when rutting.

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#### *Function of the Glands.*

I do not know who first propounded the theory that the use of the cutaneous scent-glands in Ruminants is to keep the individuals of a species together. As early as 1836 Owen discussed this view; but, finding that the glands were present in some species of Antelopes of solitary habits and absent in some gregarious forms, he dropped this hypothesis as untenable. He does not appear, however, to have attached sufficient importance to the mutual need of discovering each other on the part of the sexes of solitary species at the breeding-season, nor to the necessity of the mother and young being together, at all events

periodically, in the course of the day. A hind, for example, which leaves her newly dropped fawn in the jungle or bush while she is away feeding, must have some means of retracing her steps to the spot; and it may well be that she does so by means of the scent her own foot-tracks have left.

This obvious criticism of Owen's reasons for rejecting the theory has no doubt suggested itself to others; for the view that the secretion of the scent-glands serves to guide individuals of a species, whether gregarious or not, to one another appears to be commonly held, and was clearly expressed by Flower and Lydekker in their volume on the 'Mammalia' (pp. 315-316). That the secretion from the pedal glands must scent the ground over which the animal passes seems clear, for the pouch is commonly furnished with long hairs projecting from the orifice or the edge of the orifice, and the function of these hairs seems to be to guide the secretion downwards between the hoofs. Similarly the substance secreted by the tarsal, metatarsal, and carpal glands would touch against higher herbage, and might leave a taint behind. But the position of these glands suggests that their function is also to indicate where the animal has been lying. In the habitual resting attitude of Ruminants, the area below the knee (carpus) on both the front legs is pressed to the ground, and in the case of the Cervidæ the metatarsal gland on the outside of one hind leg and the tarsal gland on the inner side of the other in the same way come simultaneously into contact with the soil whether it be bare or overgrown with vegetation. Now the Deer which possess these glands on the hind legs have no inguinal pits or knee glands. Conversely the Bovidæ, which have no tarsal or metatarsal glands, not uncommonly possess inguinal pits and sometimes knee glands. The suggestion, therefore, is obvious that the inguinal pits of Sheep and many Antelopes, so-called, represent functionally the tarsal and metatarsal glands of the Deer and scent the ground where the animal has been lying.

It is clear that the above proposed explanation of the use of the inguinal and crural glands applies equally well to species which inhabit jungle, plain, sandy desert, or barren mountain heights. It is therefore more satisfactory than the view that the scent of the secretion is only left behind on the vegetation by the animal's passage through it. Sheep, for example, which possess inguinal glands, frequent hilly country, feeding on grass often not high enough to reach the inguinal region. Except, therefore, when these animals are in a state of repose the secretion of these glands can seldom be left behind adhering to natural objects. It is also likely that one individual can follow another or detect his whereabouts by the wafting of the scent through the air, irrespective of contact with the ground. This wafting of scent is probably the sole function of the caudal glands of Goats (*Capra*), which can in no circumstances dispose of their secretion by contact with the soil, unless a certain amount of it falls to the ground sticking to the faeces. Be it noted, too, that the habit of turning

up the tail in flight, so common in Ruminants, would expose the secretion of these glands to the air.

It has also been suggested, by Owen for example, that the use of the secretion of the pedal glands is lubrication of the hoofs. This is possible. The suggestion, however, does not exclude the explanation advocated above; and it appears to me to be probable that the function of the secretion of the pedal glands is the same as that of the carpal, tarsal, and metatarsal glands, which cannot be for lubrication. In this connection it is significant that *Epyceros* and *Tetraceros*, which have no pedal glands, have very specialised glands on the hind legs, occurring in the former above and in the latter within the false hoofs, in situations, that is to say, where the secretion must taint the ground where the animal lies.

There is a good deal of evidence that the preorbital gland has a sexual significance, at all events in part. Bennett, for example, noticed that an immature example of *Antelope cervicapra* had the lips of the sinus small and closely applied, so as to hide entirely the internal lining of the sac. In a full-grown animal, on the contrary, the sac, under the influence of excitement, was everted so as to form a projection rather than a hollow. At such times the animal delighted to rub the sac against any substance offered to it, loading it with the secretion, which had a slightly urinous odour. In a castrated individual, believed to be about the same age as the last, the gland, on the contrary, was only developed to the same extent as in the young male and was never everted as in the normal adult buck (P. Z. S. 1836, pp. 35-36). Hodgson also believed that in the Serow (*Capricornis thar*) the gland was "connected with the generative organs"; for he noticed that, in the spring especially, a thin viscid secretion was constantly poured out from the sinus, and he suggested that this profuse secretion was a means of relieving the animal during the time of extraordinary excitement to which it is liable in the breeding-season (P. Z. S. 1836, p. 39). Max Weber, moreover, has collected a good deal of evidence showing that the preorbital gland is better developed in the male than in the female of the many species of Antelope. I have noticed this myself in the case of *Raphicerus campestris* and *Tetraceros quadricornis*. I have also observed the glands of the latter species enlarge and discharge copiously in the summer, and those of specimens of *Gazella rufifrons* and *Cephalophus dorsalis* to be markedly swollen at that season. I have also seen them discharging actively in July in a female example of *Sylvicapra grimmii*, and to be quite inactive in the same animal in August. Moreover, in some Deer (*Pseudaxis* and *Rucervus*) I have noticed—and this is possibly true of all Deer—that the preorbital gland is quite small and shallow in the young as compared with the adult, a fact warranting the conclusion that this gland attains its greatest size and activity with sexual maturity.

But I cannot, on the evidence, bring myself to believe that the significance of the preorbital gland is wholly sexual. It is certain,

for example, that the gland is in some cases under the influence of other emotions than that of sexual excitement. A male Black-buck, for instance, advancing upon a man with hostile intent, turns up his tail, and everts the gland to its fullest extent; and I have seen a Sambar stag with ears pricked, nostrils dilated, and gland completely everted, gazing intently at a cat crossing the yard, his whole attitude forcibly suggestive of curiosity and doubt with a strong admixture of fear.

The habit of rubbing the secretion of the preorbital gland against the bars of cages or other objects was recorded by Bennett of *Antilope cervicapra*, by Ogilby\* of a species of Gazelle, and by Mr. Beddard† of *Oreotragus*. Ogilby, indeed, speaks of this act as frequent. In my experience it is uncommon. I have only noticed such behaviour in one Antelope, an immature example of Maxwell's Duiker, which invariably rubbed its gland against my proffered hand, exactly as a cat rubs its mouth and cheek. Considering the immaturity of the specimen in question, I cannot believe that sexual excitement was in any sense the cause of the action. It may therefore be the case, as Ogilby suggested, that "rubbing the crumens against the shrubs or stones of their desert and mountain habitats . . . may serve to direct [Antelopes] in their wanderings and migrations, when the storms and fogs incident to such places obscure all visible landmarks." As guide-marks, therefore, appeal to the sense of sight and enable the members of a species to follow one another and keep together when vision is unobstructed, so, it is believed, do the scent-glands described in this paper serve the same purpose by appealing to the sense of smell when, for any reason, free vision is prohibited.

It would be idle, however, to pretend that this hypothesis gives a full explanation of the use of the glands. It fails, for example, to account for the fact that in many, perhaps all, cases each gland emits its own peculiar scent, as recorded, for instance, of a Muntjac (*Cervulus*) and of a Gazelle (*G. dorcas*). That each scent tells its own tale to other members of the species, it is almost impossible to doubt; but what that tale may be, I am wholly unable to surmise.

#### *Origin and Evolution of the Glands.*

The preorbital glands in all the Cervidæ, and in the majority of Bovidæ that possess them, consist of an integumental thickening forming a larger or smaller invaginated sac, which serves to store the secretion. But in a few of the Bovidæ, like the Duikers (*Cephalophus*), the Gnus (*Connochates* and *Gorgon*), Buffon's Kob (*Adenota kob*), and the Sable Antelope (*Hippotragus niger*), there is no invagination, the secretion making its way directly to the exposed surface of the skin. The simplest type of preorbital

\* P. Z. S. 1840, p. 9.

† 'Mammalia,' The Cambridge Natural History, p. 13 (1902).

gland known to me is found in Buffon's Kob (*Adenota kob*) and the Sable Antelope (*Hippotragus niger*). The skin of the secreting area is merely thickened and retains its normal hairy clothing. The hairs, however, are long, forming a tuft or mat and are stuck together or hold the secretion like a scurfy powder. It is a natural inference that all the preorbital glands, however specialised, arose from simple integumental thickenings, with enlarged sebaceous and sweat-glands, resembling in essence that found in the Sable Antelope.

Exactly similar to this and equally simple in structure are the carpal or knee-glands of some Antelopes, like Gazelles and their allies, and of some Sheep, the tarsal or hock-glands of the Tele-metacarpal Cervide, and also the metatarsal glands of Deer belonging to both the divisions of this family. In some species of Deer (*Axis axis* and *porcinus*) the glandular area itself is naked and is overlapped by a fringe of long hairs surrounding it. A further stage in the evolution of this kind of leg-gland is found in the Pallah (*Epyceros*), where the glandular layer is restricted to the periphery of the area, forming an elevated ridge round it, the secretion accumulating on the smooth skin thus circumscribed.

In connection with the inguinal glands it is noticeable that they are intimately connected with the mammae. In the majority of cases their orifices are situated close to those organs, and the deepest part of the pocket actually overlies them; and when, as in *Pantholops*\*, the orifice is remote from the mamma on each side, the invagination is elongated so as to extend inwards as far as the area overlying the mamma. Again, two pairs of inguinal pouches are found only in species which have two pairs of functional mammae (*Tragelaphus*, *Redunca*).

These facts suggest that the secretion found in the inguinal sacs is derived actually from the mammary glands. This I believe to be the case; and the view is corroborated to a certain extent by the fact that the secretion in the sacs not uncommonly has an unmistakable odour of cream-cheese, or sour milk. The presence of inguinal glands in both sexes cannot be alleged as an objection to this supposition; for mammary glands are found in males as well as in females, although they are normally inoperative in the former.

It seems to me that for the origin of the pedal glands we must look to one of two processes: that is to say, they have either arisen as invaginations of the interdigital integument of a more or less fully webbed compact foot, such as is seen in *Bos*, *Taurotragus*, *Pantholops*, *Epyceros*, and others; or they are the remnants, larger or smaller according to the genus, of a primitive interdigital space.

The former explanation appears at first sight to be the more probable; and from the remark made by Flower as to the

\* But not in immature examples of *Sylvesticapra*.



seemingly primitive nature of this gland in *Paulu*, I infer that this was the view he held. If this be so, the shallow or short pocket seen in such genera, for example, as *Aleo*, *Redunca*, and *Pseudois* preceded, in an evolutionary sense, the well-developed gland possessed respectively by such genera as *Capreolus*, *Pelea*, and *Ovis*. Further, it will follow as a possibility, perhaps as a probability, that the pedal glands have been developed independently more than once in various groups of Bovidae and Cervidae; and that the genera within these families characterised by pasterns without any interdigital space have an earlier form of foot than those in which such a cleft is found: that the hind foot of *Cervus*, for instance, to take a concrete case, is more primitive than that of *Dama*.

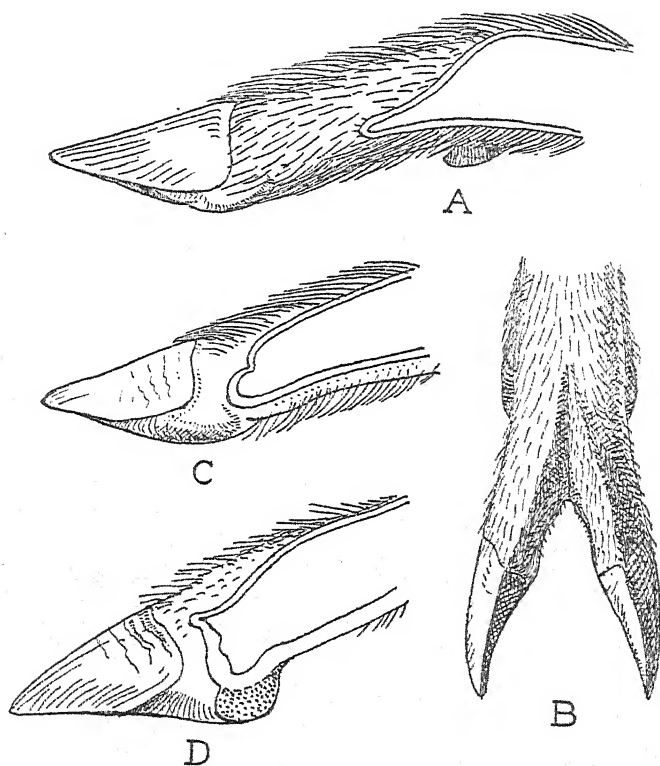
I believe this view to be erroneous; for everything we know of the evolution of the feet in Ruminantia points to the conclusion that their structural peculiarities are due to descent from four-toed feet with the phalanges separated to a greater or less extent. Gradually the lateral digits became shortened, raised from the ground, and practically functionless so far as affording support to the body was concerned. The weight was borne by the two middle toes, which became gradually strengthened for the purpose by the extension of the integument between them. Now when Mammalia of other groups develop an interdigital integument or "web," this web always, I believe, extends along the posterior or inferior aspect of the toes, leaving more or less of a cleft between them in front or above. This is well shown in such forms as *Lutra* and the Canidae and in various amphibious genera of Rodents and of other orders. For these reasons I believe that the earliest type of Ruminant foot is that in which the interdigital web consists of a fold of integument extending along the back of the pastern only, leaving a wide and deep depression between the bones above the hoofs in front. But when two surfaces of skin are opposed to form a cavity or crease, conditions favouring the activity of the skin-glands, or at all events conditions preventing the evaporation of integumental secretions, are set up. Hence, in a foot with a posterior web holding the digits together behind and a cleft between them in front, we have conditions conducive to the development of a scent-gland; and I conceive that it was from a foot of this structure, containing a potential pedal gland, that the various types of feet of the Ruminantia, whether containing glands or not, have been derived, and that the glandular pockets, whether large or small, are the remnants, specialised for the secretion of scented material, of a primitive anterior interdigital cleft.

This conception seems to me to supply the most satisfactory explanation of the prevalence and diversity of the pedal glands of the Ruminantia, all the glands being thus traceable to a common origin.

Of existing forms of this group the most primitive type of foot is found in the Tragulina, itself a primitive group combining

characters of the Suidæ, the Camelidæ, and the Cervidæ. In specimens of *Tragulus stanleyanus* (or an allied form) and of *T. meminna*, which lived in the Gardens, I find that the web on the posterior side of the pastern consists of a fold of skin which stops short at a point about halfway between the false hoofs and the heels; the back of the pastern is open in its lower half, and its front is marked with a long triangular depression, the apex of which extends up to the level of the false hoofs.

Text-fig. 141.



- A. Median vertical section of foot of *Tragulus meminna*.
- B. Anterior aspect of foot of *T. stanleyanus*.
- C. Median vertical section of foot of *Dicotyles*.
- D. The same of *Phacochoerus*.

These feet are the only ones known to me amongst the Ruminantia in which the web ceases behind far above the heels. The inner walls of the two digits of the pastern are clothed with hair, which is short and scanty in *T. stanleyanus*, longer and less

scanty in *T. meminna*\*; but I could detect no trace of any secretion indicating special activity of the skin-glands of the surfaces in question.

In the Camelidae, as exemplified by *Lama vicugna*, the foot is more specialised with respect to the extension of the web to a point halfway between the heel and the nail of the hoof; but the anterior depression on the pastern is very deep and long and glandular in its deeper portion, and the nail is small. (Text-fig. 142, A.)

Still more specialised is the foot in the Suidæ; for although there is a deeper or shallower depression on the front of the pastern, admitting of considerable distension of the hoof, the anterior and posterior walls of the pastern are widely separated and there is a strong deep interungual union extending forwards from the heels to a greater or less extent according to the species. In a Peccary (*Dicotyles collaris*) the heels were separable and the interungual union shorter and the anterior depression deeper than in a Wart-Hog (*Phacochoerus*), in which the depression was quite shallow and the interungual union long in comparison (text-fig. 142, B, D). In the foot of the Wart-Hog, moreover, which was kindly given to me by Rowland Ward, there was an actual horny union between the heels, which were thus quite inseparable. In both these species the interungual area was quite smooth; but I detected no trace of specialised glands†.

Reverting once more to the Ruminantia, I find, as is not surprising, that the foot of the Musk-Deer (*Moschus*) comes nearest to that of *Tragulus*. The pastern-web of *Moschus* nearly reaches the heels of the hoofs but not quite; the feet indeed, apart from the wealth of hair that clothes them, are like those of *Tragulus*, but very much shortened and having the glands of the depression active.

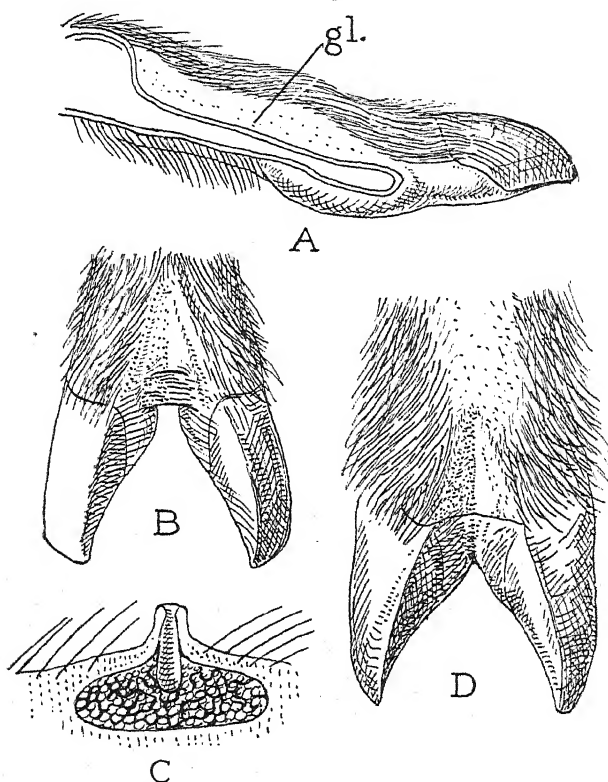
It is only a short step from the foot of *Moschus* to the hind foot of *Dama* or *Elaphodus*, the chief difference being that in these Deer the pastern-web extends right down to the heels, tying

\* In *T. stanleyanus* also the skin of the back of the pastern is coriaceous and visible through the hairs, which are as scanty as on the inner surface of this part; whereas in *T. meminna* the skin is invisible on the back of the pastern when the hairs are undisturbed. I have not investigated the submandibular glands of *Tragulus*.

† The secretion of the dorsal gland in both species of Peccary has a strong and pungent odour, like concentrated human perspiration. It may not be without significance that the scent of the South American Tree Porcupines (*Coendu villosus* and *prehensilis*) is exactly the same, as I have already recorded (P. Z. S. 1908, p. 946). And since this scent has, I believe, a warning significance in the Porcupines, it may be that we have here an instance of mimicry, Batesian or Müllerian, in smell. On the other hand, the function of the gland in the Peccary may serve the purpose merely of keeping the members of the herd together. Owen's figure and description of this dorsal gland in the Peccary are not very satisfactory. He describes and figures the gland as opening by an orifice in the mid-line of the back, without mentioning any nipple ('Anatomy of Vertebrates,' iii. p. 635, 1868). Possibly his preparation was not made from fresh material, for in the specimens I have examined the gland was marked externally by a conspicuous upstanding nipple. This was traversed by a central duct dipping into the lobular fat-like tissue of the gland. When the gland was squeezed, fluid secretion could be easily made to exude from the orifice at the summit of the nipple. (Text-fig. 142, C.)

them tightly together; and the upper portion of the interdigital cleft in front is deepened, showing the beginning of the differentiation of the glandular pouch. Hardly more advanced is the hind foot of the Muntjacs of the genus *Cervulus*, except that in *C. muntjac* part of the glandular area is markedly more pocket-like. A further stage is exemplified by the hind foot of the Hog-Deer (*A. porcinus*) and of the Axis Deer (*A. axis*), where the web

Text-fig. 142.



- A. Median vertical section of foot of *Lama vicugna*; *gl.*, glandular area.  
 B. Anterior aspect of foot of *Dicotyles collaris*.  
 C. Median vertical section of dorsal gland of the same.  
 D. Anterior aspect of foot of *Phacochærus*.

extends further forwards from the heels, holding the hoofs more securely and tightly together, the interdigital cleft being shallower owing to the greater space between the anterior and posterior walls of the pastern-web. It is quite easy to imagine the steps by which the comparatively narrow pocket-like gland of *Mazama*, *Cervulus*, and *Rangifer* has been derived from a much longer and

shallower glandular depression such as is seen in *A. aris* and *A. porcinus*; and also on the other side how by the gradual shallowing of the depression in the feet of these last-named species the condition of things found in the feet of the Red Deer (*C. elaphus*) and its allies has been reached.

I do not by any means wish to suggest that the species named stand in the exact line of descent to one another; but I do think it probable that their pedal glands represent approximately the stages through which the various types of pedal glands met with in the Cervidæ have passed in their evolution.

Similar stages in the gradual obliteration of the interdigital space accompanied by the evolution of differentiated pedal glands and their final suppression may be traced in the Bovidæ. In *Madoqua*, *Raphicerus*, and *Cephalophus*, for instance, the digits of the pastern are held together by a long and close fold of integument constituting a web which extends down or nearly down to the heels; the anterior skin of this fold forms the posterior wall of the glandular interdigital cleft, as in *Cervulus* and *Dama*. This cleft is at first open below between the hoofs and remains so in *Madoqua* and *Cephalophus*. But in both these genera, as well as in *Raphicerus* and *Dorcotragus*, the orifice of the cleft is shortened to a greater or less extent, according to the species, by the downward extension towards the hoofs of the folded integument of the anterior surface of the pastern, forming a longer or shorter anterior wall to the enclosed glandular space. Another simple modification is seen in the Gazelles, in which, while the orifice of the cleft retains almost unchanged in its original length, its inferior portion is closed and shut off from the interungual space by the anterior extension of the posterior web from the heels to the front of the hoof. Practically the same structural change has taken place in the Oribi (*Ourebia*) and in the Hartbeests (*Bubalis*, *Damaliscus*), except that in *Bubalis* the anterior web overlaps the cavity to a considerable extent above and in front.

The adult White-tailed Gnu (*Connochætes gnu*) exhibits a further stage in the evolution of the gland seen in the Hartbeest, the orifice of the cleft being still more shortened and the posterior integumental web not so closely folded. A further stage in the closing up of the orifice of the cleft is exemplified by the feet of *Oryx beisa*; and this is followed by the reduction of the orifice to a small circular aperture as in *Hippotragus*, *Pelea*, *Namorhedus*, and *Oris*; the final stage, sometimes certainly and always probably of sporadic occurrence within the limits of a species, being the retention of merely the orifice and part of the duct of the gland as in *Redunca*, *Capra*, *Hemitragus*, and *Pseudois*.

If this be the correct view of the evolution of the feet, there must be some reason or reasons for the disappearance of interdigital clefts. It seems certain that large interdigital clefts must be a source of weakness to the feet. Although a foot with its two component digits united by a close fold of integument extending from the heels up the back of the pastern is more suitable, on

account of its distensibility, for progression over soft and yielding ground than a foot with its component digits united by skin extending forwards from the heels to the front of the hoofs and restricting their separation, it is obviously less well adapted for supporting heavy weight, for speedy propulsion over hard unyielding ground, and for resisting the impact of a downward leap on a mountain side, on account of the liability to rupture of the integument under the strain put upon it.

Strengthening the feet, then, has probably been one of the factors, perhaps the principal factor, that has operated in favour of the reduction in size or total disappearance of the interdigital clefts. This theory helps to an understanding of the fact that, broadly speaking, large and heavily built Ruminants have small interdigital clefts or none, and that large interdigital clefts are for the most part found only in small animals. There are several marked exceptions to this, however, and no doubt other factors than the one suggested have influenced the formation of the feet, such as the use or uselessness of pedal scent-glands. For example, large Ruminants are much more easily kept in view by members of their own species than small ones; or, if they live in thick bush, are more easily followed by hearing as they crash away in a state of panic through the vegetation. Of these and other matters, however, we shall never have full knowledge until our information is much more exact than it is at present with respect to the senses and to the bionomics of the species concerned.

In the light of the above-made suggestions, the following considerations are worth bearing in mind :—

1. Giraffes are large, heavily built animals living in open woodland country and gallop with speed over rough uneven ground. The feet are compactly built and without interdigital clefts. The great height of Giraffes gives them considerable range of vision, enabling stragglers to keep with the rest of the herd. They can, moreover, only with difficulty and delay reach the ground with their nostrils. Hence specialised pedal scent-glands would be of little use to them for tracking.

2. All the species of *Bos* are heavily built, mostly large animals with thick legs. They live either in the open or in jungle or bush, and can be followed either by sight or by the sound they make passing through the foliage. The same applies to the Musk-Ox and to *Taurotragus*.

3. The Oryginae (*Hippotragus*, *Oryx*) are also Antelopes of large or medium size and considerable weight. The interdigital cleft is reduced to a gland with a small orifice, which is the only break in the continuity of the integument of the anterior surface of the pastern; and the orifice is smaller in the larger *Hippotragus* than in the smaller *Oryx*.

4. In the Bubalinae, large or medium-sized Antelopes, although the interdigital cleft is large and highly glandular on the front feet, it is reduced to a shallow depression on the hind feet. It is in the hind limbs that the galloping power principally lies; and

some of the Hartebeests, the Sassaby (*Damaliscus lunatus*), for example, are extraordinarily fleet of foot.

5. In the Cervicaprinæ, the larger species of *Kobus* and *Adenota* have no interdigital clefts or glands; only in the comparatively small and lightly built genus *Pelea* are the clefts retained in the form of saccular glands with a small orifice.

6. All the Duikers (Cephalophinæ) are of small or very small size and live in the forest on soft yielding ground or in fairly open country overgrown with scrub. They have large interdigital clefts and pedal glands, the scent of which is probably useful for tracking individuals concealed by the bush, through which they dive away when alarmed.

7. The Neotraginæ (*Raphicerus*, *Madoqua*, *Ourebia*) are also of small size and lightly built, and mostly frequent country overgrown with bush or scrub. They have large interdigital clefts and glands, by means of which one individual could silently follow by scent another hidden from view. *Dorcotragus*, on the contrary, lives on rocky hill-sides and has the hoofs shortened to lessen their spread at the tips, the heel-tie thickened to hold them tightly together, and the sole and heel modified to form a soft pad to break the force of a leap and prevent slipping, the interdigital cleft and gland being at the same time retained.

8. The Klipspringer (*Oreotragus*), commonly believed to be related to the Neotraginæ, although of small size and light weight, has lost the interdigital clefts. His habitat is rocky crags, where he leaps surefootedly from point to point, the hoofs although separable being firmly bound together by the thick interungual integument.

9. All the Antilopinæ (*Gazella*, *Antilope*, *Antidorcas*) live in the plains or more or less open country. They are, on the average, of small size, although larger than the Neotraginæ, and of light build, and depend for safety upon their great speed in the open. Although the interdigital clefts are large, the hoofs are held together by a fold of integument running forwards from the heels and restricting their spread to a greater extent than in the Cephalophinæ and, on the average, than in the Neotraginæ.

10. I do not know why *Ammodorcas* has lost and *Lithocranius* has retained the interdigital clefts, unless the explanation may be sought in the totally different modes of progression of the two Antelopes, which more than one observer has recorded. *Lithocranius* runs with a skulking action, ducking under the bush, with the head stretched forwards; *Ammodorcas*, on the contrary, moves with a bold stepping action, holding tail and neck erect. This at least suggests that the Dibatag is more easily kept in view by its companions than the Gerenuk, and has therefore less need of pedal scent-glands to indicate the direction taken.

11. In the Caprinæ the only wild forms which possess well-developed pedal glands belong to the genus *Ovis*, the others (*Ammodorcas*, *Pseudotis*, *Hemitragus*, and *Capra*) being without them. The latter differ markedly from Sheep in superior activity and in

their comparatively greater leaping powers, attributes which are correlated with a difference of habitat, the Goats and their allies habitually frequenting precipitous exposed rocky hill-sides or mountain heights rather than elevated plateaus intersected by ravines where Sheep are to be found. It seems to me probable that the ground frequented by Sheep is better adapted by its vegetation for holding the scent of the foot-glands and perhaps affords more cover for concealment, requiring tracking by scent, than the bare exposed situations to which the other genera are adapted.

12. In the Rupicaprinæ well-developed foot-glands occur in *Rupicapra*, *Næmoredus*, and *Capricornis*. The last two never seem to be found far from mountain forests, where individuals may easily lose sight of each other and need scent-glands to keep together. Although possessed of considerable activity and skill in covering rough ground at speed, they have not the climbing or leaping power of Goats. In this respect Chamois appear to equal Goats, and they have their feet strengthened by the forward extension of the interungual web, while retaining pedal glands which are useful perhaps in the mountain forests, where at certain times of the year Chamois resort. Although not apparently gifted with special activity or leaping power, *Oreamnos* inhabits localities right away from forests and bare of all but the scantiest vegetation. In this particular, as in the structure of their feet, they closely resemble Goats. Somewhat of a mountain-forest dweller like *Næmoredus* and *Capricornis*, *Budorcas* is nevertheless a comparatively inactive animal of large size and heavy build, requiring strong feet to carry his weight up and down the mountain-side.

13. In the Cervidæ, also, small and medium-sized animals have on the average larger interdigital clefts and more capacious glands than large animals. Very deep and long clefts with highly developed glands are found, for instance, only in small forms like *Hydropotes*, *Cervulus*, and *Elaphodus* and in the medium-sized *Dama*. Shallower but equally long clefts occur in the small *Hyelaphus* and the medium-sized *Axis*, the much larger *Rusa*, which is allied to both these genera, being devoid of them, as also are all the large Deer of the Old World. In the Telemetacarpal Deer, setting aside *Hydropotes*, there is almost always, so far as is known, a large pouch-like gland in the hind foot in genera ranging in size from the small *Mazama* to the large *Rangifer*, two exceptions being the diminutive *Pudu*, in which the glands are aborted, and the giant *Alce*, in which the gland is considerably reduced.

Very little is unfortunately known about the habitat of *Pudu* beyond the fact that it has been recorded from Ecuador and the Chilian Andes and appears to live normally at tolerably high altitudes. From its compactly built feet, I infer that this little Deer frequents hard or stony ground requiring firmly welded hoofs. If this be so, we find a reason for the disappearance of the glandular pouch in the feet found in its ally *Mazama*.



if there is any truth in the supposition that such pouches are a source of weakness.

In the case of *Alce* the nearly vestigial nature of the pedal gland is accompanied by two features in this genus which have an interesting bearing on the suggestions here put forward to account for the retention or loss of interdigital clefts and glands. In the first place, this Deer is of great stature and weight, the latter requiring strong feet for support and the former making concealment from sight, involving the necessity of tracking by scent, less likely than in the case of smaller animals. In the second place, length of limb is correlated with shortness of neck, so that the Moose can only with difficulty reach the ground with its nose. Scent-tracks left by the feet, therefore, would be of comparatively little use in enabling one Moose to find another.

No Deer known to me have such strongly built completely webbed feet as are found in the large Bovidæ like *Taurotragus* and *Bos*, or indeed as in some of the smaller members of that family, like *Tetracerus* and *Oreotragus*. Generally speaking, there is a greater tendency towards plantigradism and there is nearly always a more marked depression on the front of the pastern. This is to be attributed, I suppose, to the circumstance that Deer are for the most part denizens of woodland country, woods, jungle, or swamps, where the soil is usually softish and yielding. This brings us to the fact, otherwise perhaps seemingly opposed to the suggestion here made as to the cause conducing to the suppression of the pedal gland in the hind foot, that a large and heavily built animal like the Reindeer none the less retains a well-developed glandular pouch. The Reindeer, however, has a foot eminently adapted for traversing soft ground, whether it be snow or swamp, and does not require a foot of such strength as to call for the suppression of the glandular pouch.

That the Cervidæ, like the Bovidæ, originally possessed interdigital clefts and glands on the front as well as on the hind feet is probable on general grounds, and also from the fact that a gland is retained on the front foot in a state of greater or lesser development in some American Deer, while a moderately deep cleft is present on the front foot of *Dama*. The only suggestion I can at present make to account for the greater compactness of the fore feet as compared with the hind feet is the fact that all Deer, I believe, both stags and hinds, commonly use their fore feet both in attack and defence, dealing blows with great precision, swiftness, and strength. This I have myself witnessed on more than one occasion. For such a purpose it seems obvious that a strongly built foot is required.

These brief comments on the bionomics of Ruminants indicate in a general way the lines along which research, likely to lead to a better understanding of the structure of the feet and the reasons for the retention or loss of the pedal glands, may probably, I think, be pursued with profit.

## 2. On a Wapiti and a Muntjac.

By R. LYDEKKER\*.

[Received May 4, 1910.]

(Text-figures 143 &amp; 144.)

THE WAPITI (*Cervus canadensis wardi*, subsp. n.).

A few weeks ago the Rev. W. N. Fergusson, a missionary in Sze-chuen, returned from China, bringing with him a small collection of Mammals from that province and Tibet, among them being a skin of *Eluopus* and a pair of antlers of the Sze-chuen Sambar (*Cervus unicolor dejeani*). The collection also included two shed antlers of an adult Wapiti (text-fig. 143), which may or may not be a real pair, although from the fact that neither is quite symmetrical in form and size with its fellow, while one is redder than the other, there seems considerable probability that the two are not naturally associated. These antlers, I was informed at the outset, came from Tibet, and, owing to the fact that Wapiti and other antlers (although generally, if not invariably, in the velvet) constitute an important article of export from the Altai and elsewhere to China, I was naturally suspicious—especially as Wapiti have been hitherto unknown to exist on the southern side of the Gobi—that Mr. Fergusson's specimens might have been imported into Tibet.

Enquiries were accordingly made from their owner as to the history of the specimens, to which Mr. Fergusson replied as follows:—

“As you are no doubt aware, the native haunts of the Parti-coloured Bear (*Eluopus*) are in the dwarf bamboo and rhododendron forests so abundant in Sze-chuen at an elevation of from 9000 to 11,000 feet above sea-level. The Deer you identify as Wapiti inhabit the region just above the tree-line; I have never shot one myself in these regions, yet I have it on good authority that they have been obtained. The specimen sent to you I obtained from a native hunter within fifty miles of the place where the Parti-coloured Bear was shot. The Deer, of course, never enter the bamboo-thickets in which the Bear makes its home, but graze on the grassy plains beyond.”

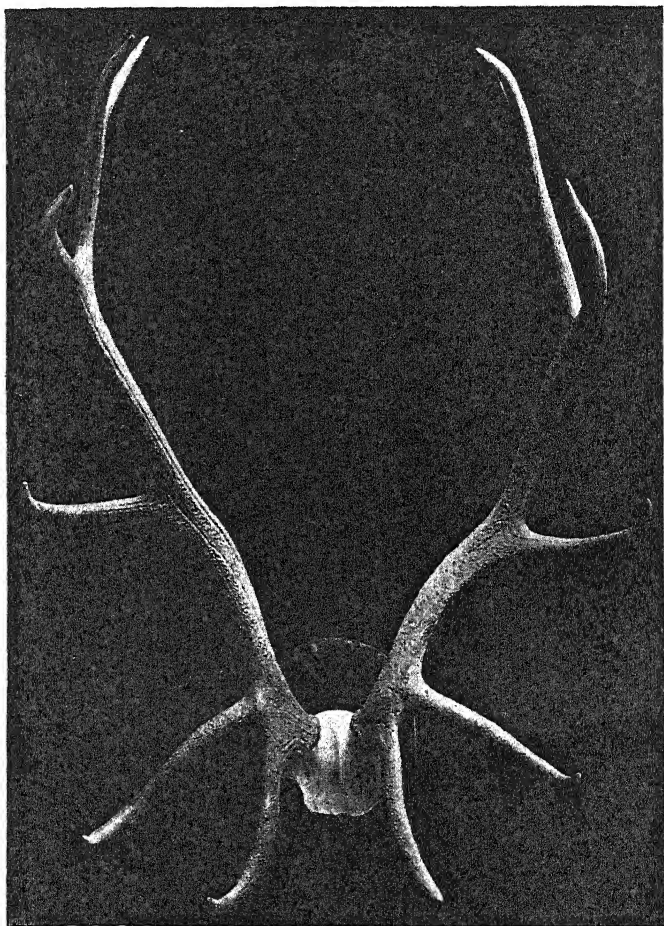
Although the Deer referred to by Mr. Fergusson may have been the so-called White Deer or Sze-chuen Hangul described by myself in the Society's ‘Proceedings’ for 1909 (p. 588) as *Cervus cashmirianus macneilli*†, the late Mr. J. W. Brooke referred to another and apparently larger Deer as inhabiting the Sze-chuen frontier, and there accordingly seems to be a probability that the story told by the native hunter to Mr. Fergusson

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† Since this paper was written, Major McNeill has informed me that the specimen was shot on the Tibetan side of the border.

may be true; the fact that the antlers are shed, and perhaps odd ones, by no means necessarily discrediting the narrative.

Text-fig. 143.



Antlers of Tibetan Wapiti, *Cervus canadensis wardi*.

That a representative of the Wapiti should be found on the mountains to the southward of the Gobi Desert is rendered probable—or, at all events, not improbable—by the case of the Argali Sheep (*Ovis ammon*), whose distribution (if *poli* and the other allied forms be regarded as local races) surrounds the Gobi.

Here it is my pleasant duty to record an act of special liberality on the part of Mr. Rowland Ward, F.Z.S., who, when their interest was brought to his notice, purchased the two antlers and presented them to the British Museum.

As is apparent from the text-figure, the antlers are unmistakably those of a Wapiti, and are somewhat inferior in point of size to the pair surmounting a specimen of the Tian Shan race exhibited in the Natural History Museum. Satisfactorily to distinguish some of the races of Wapiti by their antlers alone, I find an exceedingly difficult, if not actually impossible, task. Nevertheless, when the antlers forming the subject of this paper are placed alongside Wapiti antlers from the Altai and Tian Shan, it will be found that they differ in certain small details from all; although such slight differences are almost impossible to describe. One recognisable feature seems, however, to be the narrowness of the terminal fork, as compared with that of a Tian Shan Wapiti.

If I am right in regarding these antlers as indicating the existence of a Tibetan Wapiti, it is a practical certainty that this animal will represent a race by itself; and although I am not at present in a position to define it, I venture to propose the name of *Cervus canadensis wardi* for this presumed new race, in honour of the donor of the type specimen.

THE MUNTJAC (*Cervulus bridgmani*\*, Lydekker, Abstract  
P. Z. S. 1910, p. 38).

Passing on to the subject of the second part of this paper, I have first of all to express my thanks to Lieut. the Hon. R. O. B. Bridgeman, R.N., F.Z.S., for submitting to me a series of skins and skulls of Muntjacs from the An-wei district of Western China, obtained by himself during a shooting trip. Mr. Bridgeman is of opinion that there are three distinct kinds of Muntjac in An-wei, which he calls the red, the black, and the yellow or tawny; the last being the smallest.

Of these, the so-called red species is identified, and rightly, by Mr. Bridgeman with *Cervulus sclateri*, which appears to be distinguished from *C. lachrymans* of Sze-chuen by the more marked contrast between the yellow of the head and the rufous or olive of the neck. Both are characterised by the absence of a dark nuchal stripe; while in *sclateri*, at any rate, the young are spotted, instead of uniformly coloured as in *reevesi*. The backs of the ears are, I believe, yellow in both sexes. In An-wei *sclateri* is the common species.

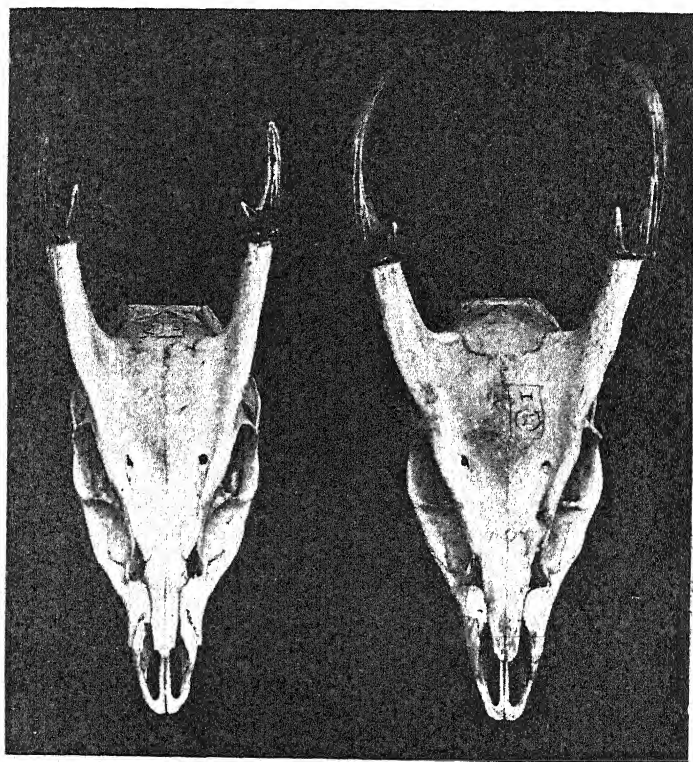
With regard to Mr. Bridgeman's "yellow species," in which the whole tone of the coat is yellowish olive, with yellow speckles on the hair, I take this to be near akin to *C. reevesi*, which is, however, described as being typically reddish chestnut speckled

\* The complete account of this new species appears here; but the name and a preliminary description were published in the 'Abstract,' No. 86, 1910.

with yellowish grey. A mounted specimen in the Museum is darker, with rufous speckles, which almost disappear on the hind-quarters. All show a dark nape-stripe.

Mr. Bridgeman's yellow Muntjac agrees with *reevesi* in the relatively small degree of divergence of the antler-pedicles (text-fig. 144, A), the great size of the lachrymal fossa, and the presence of a distinct outer lateral prominence on the nasals where they first come into contact with the maxillæ.

Text-fig. 144.



A

B

Skulls of Chinese Muntjacs.

A. *Cervulus reevesi* (?). B. *Cervulus bridgemani*.

In the male skin the back of the ears is covered with yellow hairs, whereas in the female the hairs on this part are blackish. No such difference appears to have been described between the ears of the two sexes of *reevesi*; but this may possibly have been

overlooked. For the present, at any rate, I must leave this yellow Muntjac without a definite name, suggesting, however, that it is a local race of *reevesi*.

Of the black, or, as it might preferably be called, the brown Muntjac, Mr. Bridgeman has sent home the skins and skulls of several specimens of both sexes. The general type of colouring of the fur of the upper parts is the same as in the yellow Muntjac, but the tint is much darker. In the male the fur is blackish brown, with the hairs on the middle line of the back and the whole of the rump faintly ringed with yellow. In the female the yellow rings on the hairs are more numerous and brighter in colour, while the annulated area extends down to the flanks, so that the whole body is gold-speckled. In both sexes there is a dark nuchal stripe; and in the female, like that of *reevesi*, the black frontal lines unite into a broad patch between the ears, which is continued as the nuchal stripe. In the female the ears are black externally, whereas in the males they are yellow, although with the basal half black in one example.

The skull (text-fig. 144, B), while agreeing with that of the yellow Muntjac in the great size of the lachrymal fossa, differs in many instances, at any rate, by the greater divergence of the antler-pedicles, and the invariable absence of any distinct lateral projection on the nasals where they first come into contact with the maxillæ.

This Muntjac appears to be a new form, which I propose to regard as a species, with the name of *C. bridgemani*, although it may be only a larger race of *reevesi*. The mounted female presented to the Museum by Mr. Bridgeman is the type. The height of this specimen is 19 inches, and when freshly killed its weight was 29 lbs.

These brown Muntjacs live normally at a high elevation in the Wei-Yas Shan Mountains of An-wei; and descend to the low grounds only during spells of exceptional cold in mid-winter. Information of their existence was given to Mr. Bridgeman by Mr. Charles Maguire, a mining agent in An-wei; and the donor suggested that the species should be named after that gentleman, although this appeared to me, on the whole, inadvisable\*.

These Muntjacs belong to the typical group of the genus, in which the upper surface of the tail is chestnut; but in their generally dark colour, and especially in the black ears of the female, they form in some degree a transition to the plum-coloured group, in which the upper surface of the tail is dark; the next connecting species being *C. fæa* of Tenasserim, which lacks the head-crest of the Chinese *crinifrons* and the allied genus *Elaphodus*.

It may be added that I have given preliminary notices—without specific names—of both the Wapiti and the Muntjac in the 'Field' newspaper for April 1910.

\* A male skin shot by Mr. Maguire was received at the British Museum after this paper was read.

## 3. On Three African Buffaloes.

By R. LYDEKKER \*.

[Received May 12, 1910.]

(Text-figures 145-148.)

In the present communication I take the opportunity of giving figures of the heads or horns of three races of African Buffaloes, two of which, in my opinion, indicate types distinct from any of those described by Dr. P. Matschie in his paper on the local forms of African Buffaloes published in the 'Sitzungsberichte Ges. Naturfor.,' Berlin, 1906.

## 1. BOS CAFFER THIERRYI Matschie.

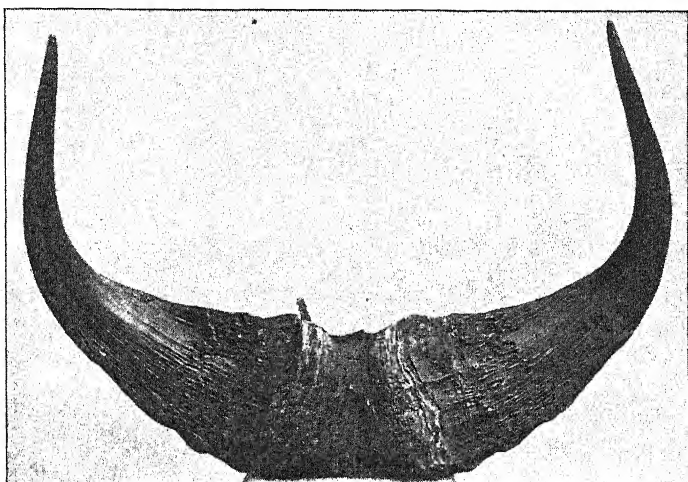
As announced in the 'Daily Telegraph' of December 30th, 1909, Dr. K. W. Kumm, during his journey through equatorial Africa from Lake Chad to Wau, obtained evidence of the existence in the Upper Shari Valley of what he at the time regarded as a new Buffalo. This portion of the Shari Valley, it may be well to mention, is situated in the French Congo, somewhat to the northward, so far as I can determine from the narrative, of an east-and-west line connecting Adamawa, in the German Cameruns, with the British station of Wau, in the Bahr-el-Ghazal. The single trophy of this Shari Buffalo brought home (and presented to the British Museum) by Dr. Kumm consists of the frontlet and horns of an adult, but not aged, bull (text-fig. 145). The animal to which the specimen belonged appears to have been killed at a comparatively recent date, but not, I should say, by a European; and the long, sharp tips of the horns afford decisive evidence as to its relative age.

In the fact that they are situated throughout their length almost in one plane, coupled with the great length of the slender, cylindrical tips, which exceeds that of the basal portion, and the right angle formed by the junction of these two portions with one another, the Shari horns accord with the pair from the interior of Togoland, German West Africa, described and figured by Dr. Matschie on page 172, fig. 3, of the paper already cited, under the name of *Bubalus thierryi*. The Shari horns are, however, much deeper in the antero-posterior direction at their bases, where they are more expanded and flattened, and also much more closely approximated in the middle line than in the type of *thierryi*. The latter is, however, a female, and this being so, there seems no reason why the Shari horns should not pertain to the same race. Accordingly, despite the long interval between the localities where the two specimens were obtained, there seems no possibility of separating the Shari horns from *thierryi*, and I therefore associate them provisionally with that race.

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The horns of the Lake Chad *B. c. brachyceros* are of a much smaller and totally different type; while those of the Senegambian *B. c. planiceros*, according to the specimen figured on page 105 of my 'Wild Oxen, Sheep, and Goats,' have, even when unworn, much shorter tips.

Text-fig. 145.



Frontlet and horns of bull of *Bos caffer thierryi*.  
From Dr. Kumm's specimen in the British Museum.

The horns of Dr. Kumm's specimen have a length of  $31\frac{1}{4}$  inches along the outer curve, with a basal span of 8 inches, and a tip to tip interval of  $26\frac{1}{2}$  inches.

## 2. *BOS CAFFER SIMPSONI*, subsp. n.

On page 156 of vol. cxv. of the 'Field' newspaper for 1910, I gave a preliminary notice, accompanied by a figure, of certain Buffalo-heads obtained by Mr. M. W. Hilton-Simpson on the left bank of the Kwilu River in the Belgian (not, as I first thought, the French) Congo. This river, which takes its rise in Portuguese territory, runs nearly due north, and discharges into the Kwango, a tributary of the Kasai, which, in its turn, forms the most important affluent of the Congo. Of these Buffaloes, which were found in herds of considerable size, the heads of two bulls and two females were brought home by Mr. Hilton-Simpson, and of these one female has been presented to the British Museum.

In the heavily fringed ears and the general form of the horns these Buffaloes approximate to the well-known red Congo Buffalo (*B. c. nanus*); but the horn-measurements of the largest bull



(text-fig. 146) exceed any recorded for the latter race, the right horn measuring  $25\frac{3}{8}$  inches along the outer curve and the left one  $24\frac{1}{2}$  inches; the basal girth of the former being  $16\frac{1}{2}$  inches, its maximum width  $6\frac{3}{8}$  inches, and the expanse from tip to tip  $13\frac{1}{2}$  inches. In the largest cow (text-fig. 147) the left horn measures 15 inches in length, with a girth of  $9\frac{1}{2}$  and an expanse of  $8\frac{3}{4}$  inches. In profile the horns incline upwards nearly in the plane of the face.

Text-fig. 146.

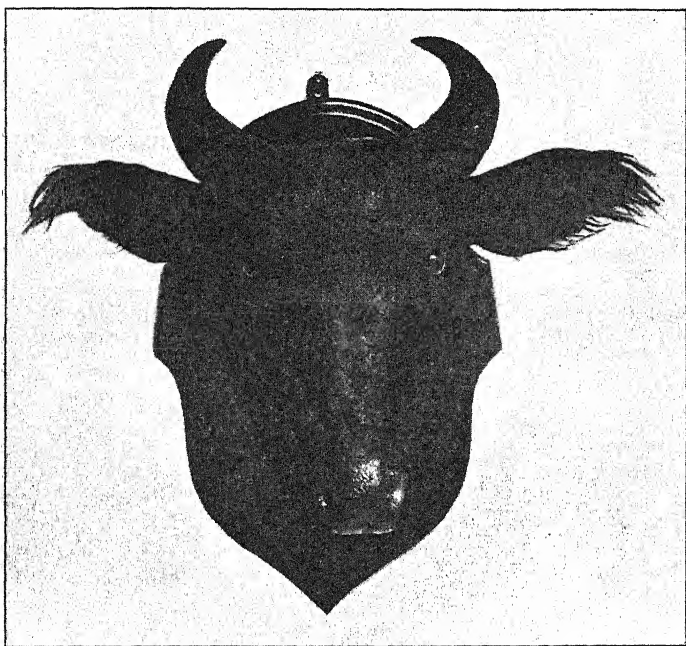


Head of bull *Bos caffer simpsoni*. From Mr. Hilton-Simpson's specimen.

The colour of both cows and bulls is a pure brown, and thus much darker than the tawny red of *nanus*; the young only agreeing approximately in hue with the latter, and the cows being fully as dark as the bulls. Except in the bull whose head is shown in text-fig. 146, the fringes of the ears are tinged with tawny, with one white lock. In size, Mr. Simpson estimates that the Kwilu Buffalo slightly exceeds the specimens of the red Congo race mounted in the British Museum.

That the Kwilu Buffalo is distinct from *B. c. nanus*, whose habitat includes Nigeria, Ashanti, and Sierra Leone, seems to be clearly indicated by its darker colour and larger horns, the form of which does not agree precisely with those of any example of the latter that have come under my notice; and I cannot identify it with any of the other races at present. Accordingly, I propose to regard it as representing a distinct race, under the name of *Bos caffer simpsoni*; taking as the type the head of a cow which Mr. Hilton-Simpson has presented to the British Museum.

Text-fig. 147.



Head of cow *Bos caffer simpsoni*. From Mr. Hilton-Simpson's specimen.

The Kwilu Buffalo evidently forms a connecting-link between *B. c. nanus* and the short-horned blackish races of *Bos caffer*, as exemplified by a pair mentioned by Dr. Graham Renshaw in the Society's 'Proceedings' for 1904, p. 130, as being then living in the Antwerp Zoological Gardens. Those animals appear to have had horns of the same general type as those of the Kwilu race, but their general body-colour was much darker, being described as dark blackish brown; the ears show similar heavy fringes. As suggested by Dr. Renshaw, these Buffaloes may have been the Senegambian *B. c. planiceros*.

3. *BOS CAFFER COTTONI* (?) Lydekker.

So far as my information goes, the small-horned *Bos caffer brachyceros* is at the present time known only by the two type skulls brought home by Messrs. Denham and Clapperton after their journey through the Lake Chad district, and named and described by Dr. Gray in the 'Annals & Magazine of Natural History' for 1837, vol. i. p. 587. As to the precise locality where this so-called Lake Chad Buffalo was obtained, there is no definite information, the original description merely mentioning "Central Africa": accordingly, the spot may well have been scores of miles distant from the Lake. In 'Wild Oxen, Sheep, and Goats' I have tentatively regarded the two type skulls as respectively representing the bull and cow of the Lake Chad race; and I am now more convinced than ever of the correctness of this interpretation. A figure of the skull of the bull, which is fully adult, will be found on page 114 of the volume cited

Text-fig. 148.

*Bos caffer cottoni* (?). Head of young male.

From the specimen in the British Museum.

This skull is characterised by the shortness and generally small size of the horns, which are separated by a wide gap in the middle line of the forehead, and show no marked expansion or prominence at the base. Their basal portion, which presents a nearly flat front surface, ascends upwards and outwards

at an angle of almost exactly  $45^{\circ}$  with the middle line of the skull for some distance, after which the horns are curved inwards in a regular sweep, so that the tips (which are quite unworn in the specimens) are directed inwards in a nearly horizontal plane. In my judgment, this type of horn is quite distinct from that of both *B. c. nanus* and *B. c. planiceros*.

Thus matters stood till 1907, when Prince E. Demidoff presented to the British Museum the head of an immature bull Buffalo belonging to one of the little-known reddish races, shot by his brother, the late Prince Paul Demidoff, somewhere in the interior of the French Congo. The immature condition of the horns in this specimen (text-fig. 148) is extremely unfortunate, and led me at first to the conclusion that they indicated a short-horned race, with a large interval on the forehead between the horns of opposite sides, and a horn-curvature which would probably grow into that of *brachyceros*; but a specimen from the same district shown me by Mr. Rowland Ward proves this to be wrong. In colour the abundant hair of Prince Demidoff's specimen is decidedly darker than that of the bull *nanus* from Ashanti exhibited in the Museum; its general tint being tawny brown, tending to blackish or black on the muzzle and chin. The most characteristic feature of the specimen is, however, the colour of the excessively abundant fringe of long hair on the margin of the ears. At the base of the upper edge the colour of these hairs is light yellowish chestnut; but on the remainder of the same margin, together with most of the lower ones, the hairs are black, with two small flecks of straw-colour near the middle of the lower border and a larger patch near the base of the same. In these respects the ear-fringes differ in colour from those of *B. c. nanus*. The specimen shown me by Mr. Ward is an older bull, in which the colour of the hair is bright red, while the horns, although smaller and more separated on the forehead, are of the type of those of *B. c. typicus*. This head indicates a race allied to or identical with my *B. c. cottoni* from the Semliki (P. Z. S. 1906, p. 996).

POSTSCRIPT.—Since this paper was read I have received evidence of the existence of another, and very well-defined, race of dwarf Buffalo, inhabiting the Yala district of South Nigeria, and characterised by the bulls being brownish black and the cows dun or khaki-coloured. Heads of a bull and cow were brought home by Mr. J. H. L. Thompson, of the Duke of Wellington's Regiment, and have been mounted at Mr. Rowland Ward's establishment. Mr. Thompson informs me that the bulls of this race stand from 3 ft. 6 in to 4 ft. at the withers, and that they are short-legged and heavily built animals. In the adults of both sexes the legs are light-coloured from the knees and hocks to the hoofs. The calves are dark grey.

My informant also states that there occurs a larger race of

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Buffaloes in the same district, whose colour is darkish rufous, with the lower portions of the legs rather lighter than the body.

Although I am fully convinced of the distinctness of the small Yala race, I do not propose to give it a name until a specimen of the head of at least one of the sexes is available for the British Museum. A fuller account will be found in the 'Field,' vol. cxv. p. 1112, 1910.

#### 4. On a new Antelope and on the Spanish Chamois.

By Prof. A. CABRERA, C.M.Z.S.

[Received May 10, 1910.]

(Text-figure 149.)

Among a great number of hunting-trophies obtained last winter by the Spanish sportsman, Mr. Ricardo de la Huerta, during an expedition in British East Africa, there are two Antelope heads which seem to represent a new form of *Damaliscus*. They belong, indeed, to animals similar in size and colour to *D. jimela*, but with the middle part of the face not black, but pale whitish buff. That they are not individual aberrations is demonstrated by the fact that Mr. de la Huerta has met with two herds entirely composed of pale blazed Topis—one on the Uasingishu plateau and another near the Turkwell River. According to the natives, these antelopes were also seen by the Roosevelt party, but no specimens were obtained.

Without entering now into the question whether it is a true species or only a local race of *Damaliscus corrigum*, I think this form with whitish forehead needs a name, and I propose to call it *Damaliscus phalius*\*.

I take this opportunity to describe and name also the Chamois from the Cantabrian Mountains, N. Spain, which is a very different form from the Pyrenean one (*Rupicapra rupicapra pyrenaica* Bonap.), smaller in size and redder in colour.

Following are the brief descriptions of these two new animals.

##### *DAMALISCUS PHALIUS*, sp. n.

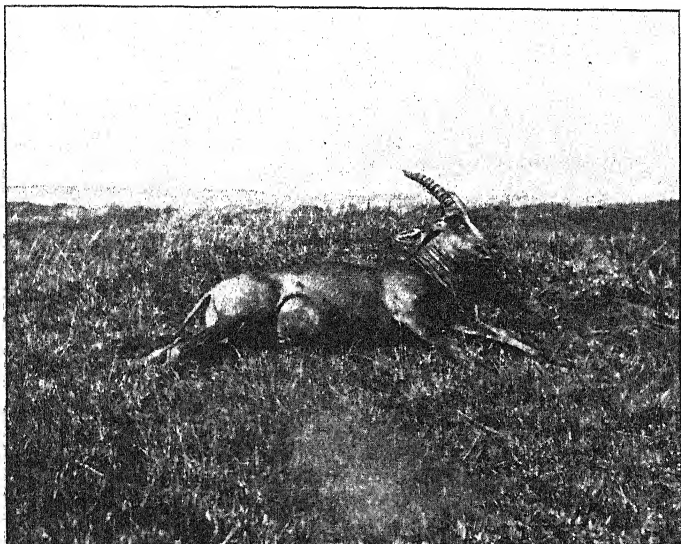
Similar to *D. jimela* in size and in the colour of the body and limbs, but with a pale whitish-buff blaze on the face, instead of the black one common to the other forms of the *corrigum* group. In old males, according to Mr. de la Huerta, the blaze becomes pure white and almost as well defined as in *D. albifrons* and *D. pygargus*.

*Hab.* The north-western part of British East Africa, east of Mount Elgon.

\* *Phalius* was, according to Dr. Ridgeway, the Greek name for a dark-coloured horse with a white blaze from the top of the head down to the nose.

The type is the specimen from Uasingishu in the collection of Mr. de la Huerta (text-fig. 149). It is an adult, but not old, male, with horns 432 mm. in length along the front curve. The Turkwell River specimen is a female.

Text-fig. 149.



Whitish-blazed Topi (*Damaliscus phalius*) from the Uasingishu plateau. Type.

*RUPICAPRA RUPICAPRA PARVA*, subsp. n.

Smaller than all the other forms of the species. General colour brownish red, darker on the limbs, becoming dark brown on the forearms, above the "knees," and on the inner part of the hind limbs. Sides of the head dirty greyish brown, leaving in the middle of the face a broad space of yellowish buff. The throat and under jaw are not whitish, as in *R. r. pyrenaica*, but only a little paler than the body-colour.

*Hab.* Cantabrian Mountains, N. Spain.

The type is a female from Picos de Europa, Santander province, in the Madrid Museum of Natural History. She is 570 mm. in height to the shoulder, with horns 146 mm. in length on the front curve. The horns of a male skull in the same collection are stouter, but not longer. A female from the Pyrenees, also in the Madrid Museum, is 690 mm. in height to the shoulder, and has horns 232 mm. in length.

5. The Changes of Plumage in the Red Grouse (*Lagopus scoticus* Lath.) in Health and in Disease. By EDWARD A. WILSON, M.B., F.Z.S., Field-Observer to the Grouse Disease Inquiry.\*

[Received June 14, 1910.]

(Plates LXXVIII.-CI.† & Text-figure 150.)

#### PART I.

##### *Plumage Changes in the Cock Grouse.*

When a large number of skins of the cock Grouse are arranged together, side by side, according to the month of the year in which the birds were killed, it will be found that, even taking into account the differences of well-marked local variations in plumage, the series can readily be divided into two very distinct sets.

There is first a very marked uniformity in the plumage of the cock birds killed from the middle of November to the end of June; and likewise amongst those killed from the end of June to the middle of November.

These two periods, November to June and June to November, mark the two seasonal changes of plumage in the cock Grouse.

*The first is a plumage worn throughout the winter, as well as during the courting- and breeding-season of the spring.*

*The second is a plumage worn throughout the summer and autumn.*

It is necessary to lay stress upon this general broad division of the cock Grouse's plumage, and if a large number of skins can be arranged as suggested, the exact time at which the Grouse has definitely changed from the one plumage to the other cannot possibly be overlooked. The birds obtained at the end of May are definitely in the darker and redder winter-plumage, and those procured at the end of June are definitely in the paler and more buff-coloured summer-plumage; those killed at the beginning of October are still partly in the paler summer-plumage, and by the end of November all are in the darker winter-plumage.

It must, however, be added, that there is hardly a month in the whole year, or a Grouse-skin in a collection of many hundreds covering every month of the year, in which one plumage only can be found unmixed with the other. This fact accounts largely for the misunderstanding which at one time existed, but which has now, we hope, been satisfactorily settled, in respect of the whole

\* Owing to Dr. Wilson having left London on the Antarctic Expedition before this Memoir was set up in type, he was unable to revise the proofs, but left full power to the Editor and Mr. W. R. Ogilvie-Grant, who have made certain modifications in the text.

† For explanation of the Plates see p. 1032.



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PAIR OF RED GROUSE IN SUMMER WITH YOUNG CHICKS.



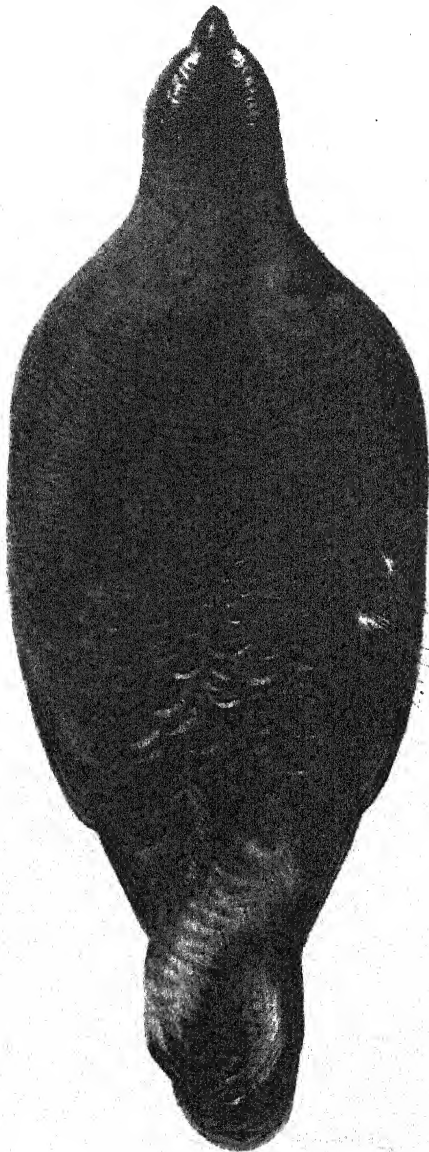




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MALE GROUSE, BLACK TYPE, IN FULL WINTER-PLUMAGE.

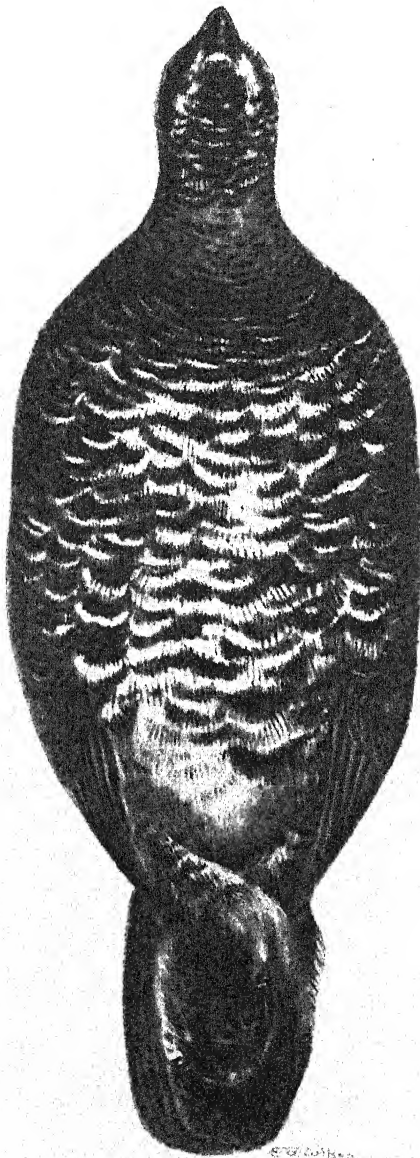




Andre & Sleigh, Ltd.

MALE GROUSE, RED TYPE, IN FULL WINTER-PLUMAGE.





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MALE GROUSE. WHITE-SPOTTED BIRD OF THE RED TYPE.





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MALE GROUSE, RED TYPE, IN FULL WINTER-PLUMAGE WITH A  
FEW BLACK-CENTERED FEATHERS OF THE PREVIOUS  
AUTUMN-PLUMAGE.



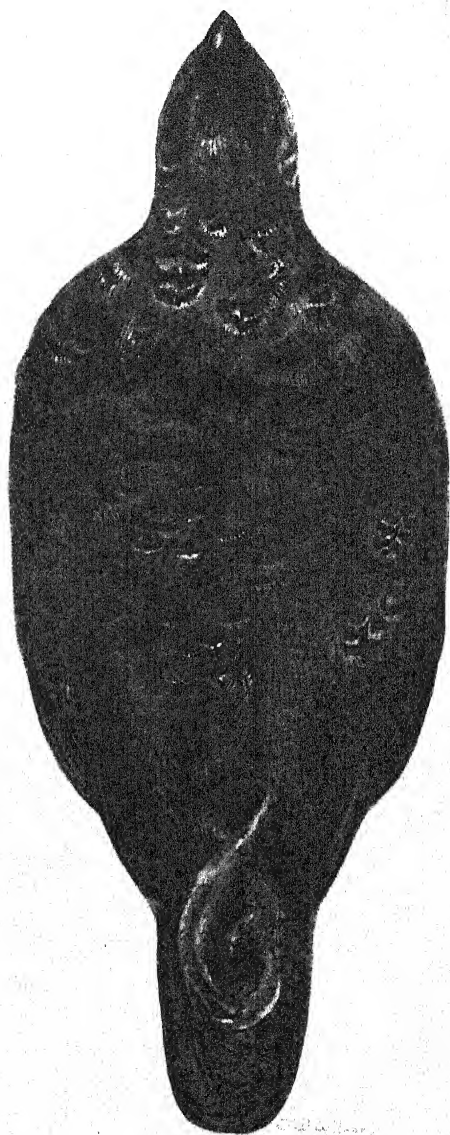




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MALE GROUSE SHOWING MARKED BEGINNING OF THE  
AUTUMN-PLUMAGE ON HEAD AND NECK.

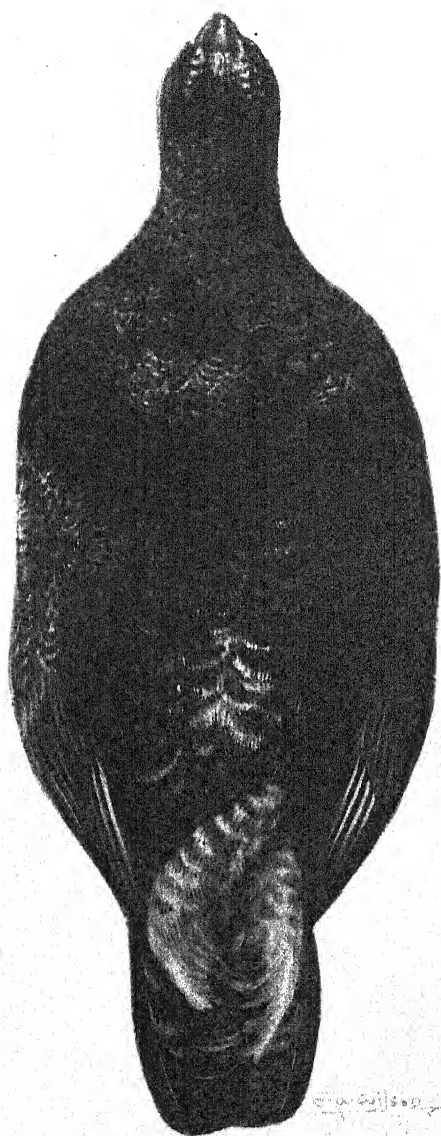




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MALE GROUSE CHANGING FROM WINTER- TO AUTUMN-PLUMAGE.

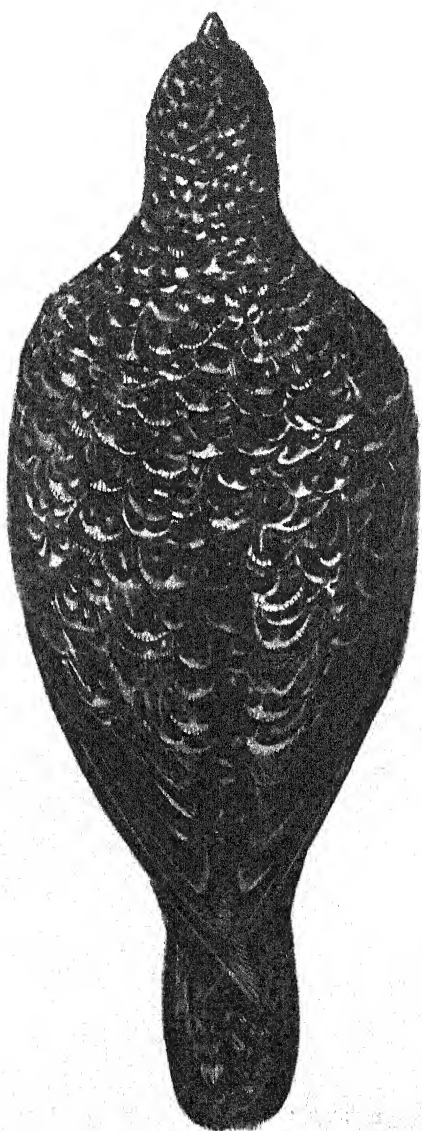




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FEMALE GROUSE, BLACK TYPE, IN AUTUMN-PLUMAGE.



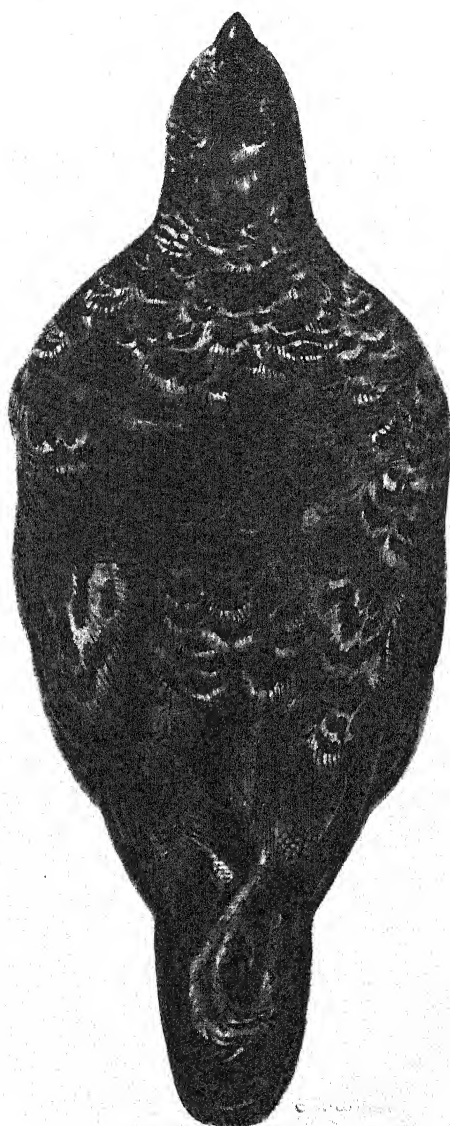


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FEMALE GROUSE IN FULL BREEDING-PLUMAGE.



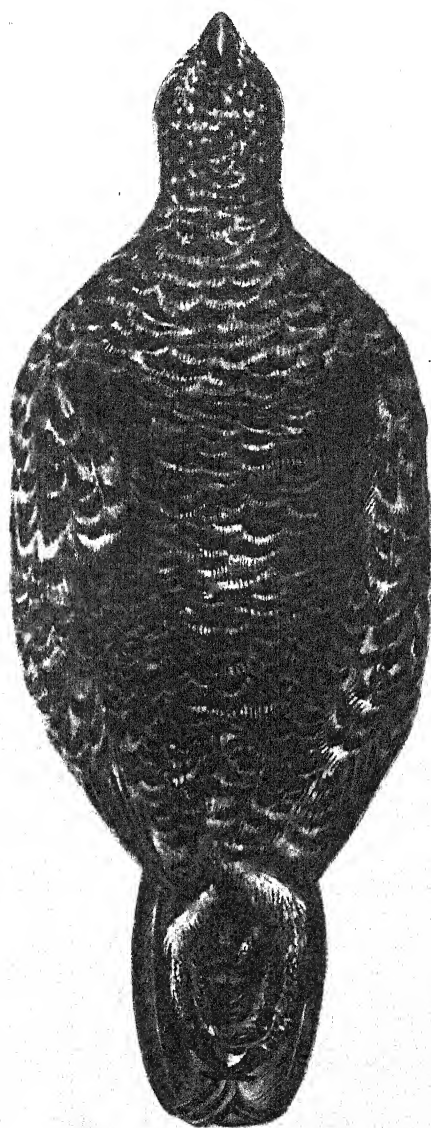




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FEMALE GROUSE, RED TYPE, CHANGING FROM WINTER- TO  
SUMMER-PLUMAGE.



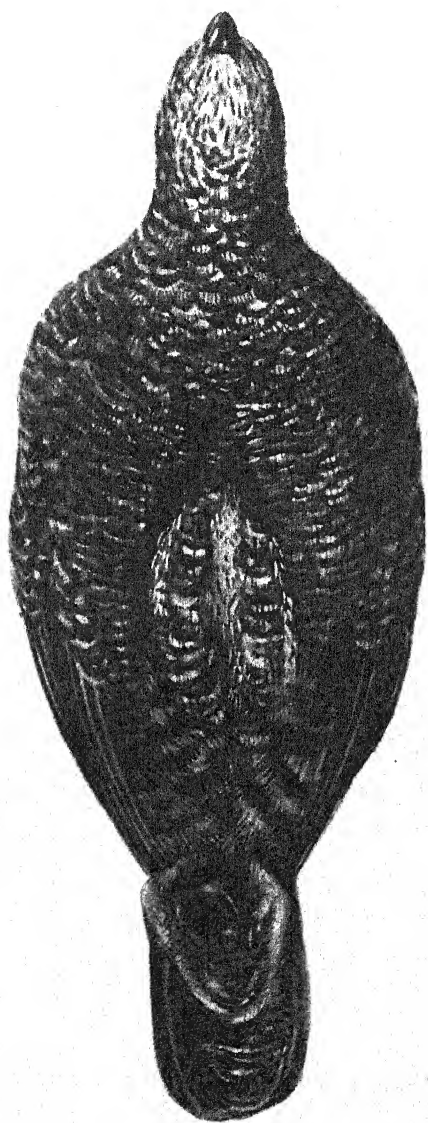


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Andre & Seigh, Ltd.

FEMALE GROUSE IN FULL SUMMER-PLUMAGE.

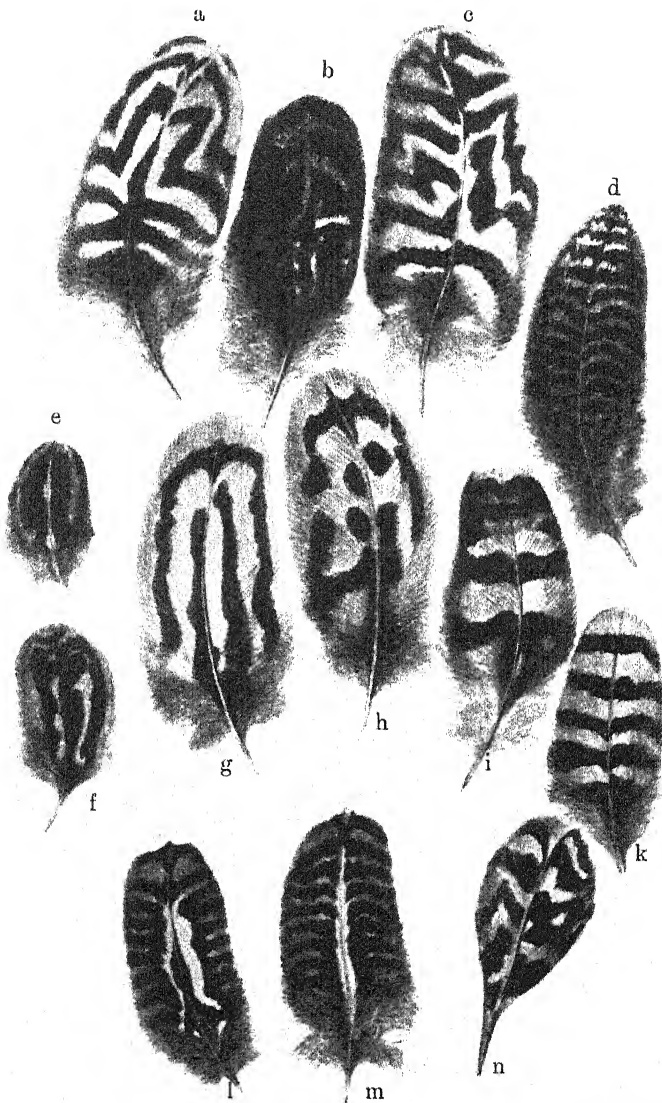




Andre & Seigh, Ltd.

FEMALE GROUSE SHOWING BARE PATCH OF SKIN AND DOUBLE  
LINE OF BARRED FEATHERS ON ABDOMEN.



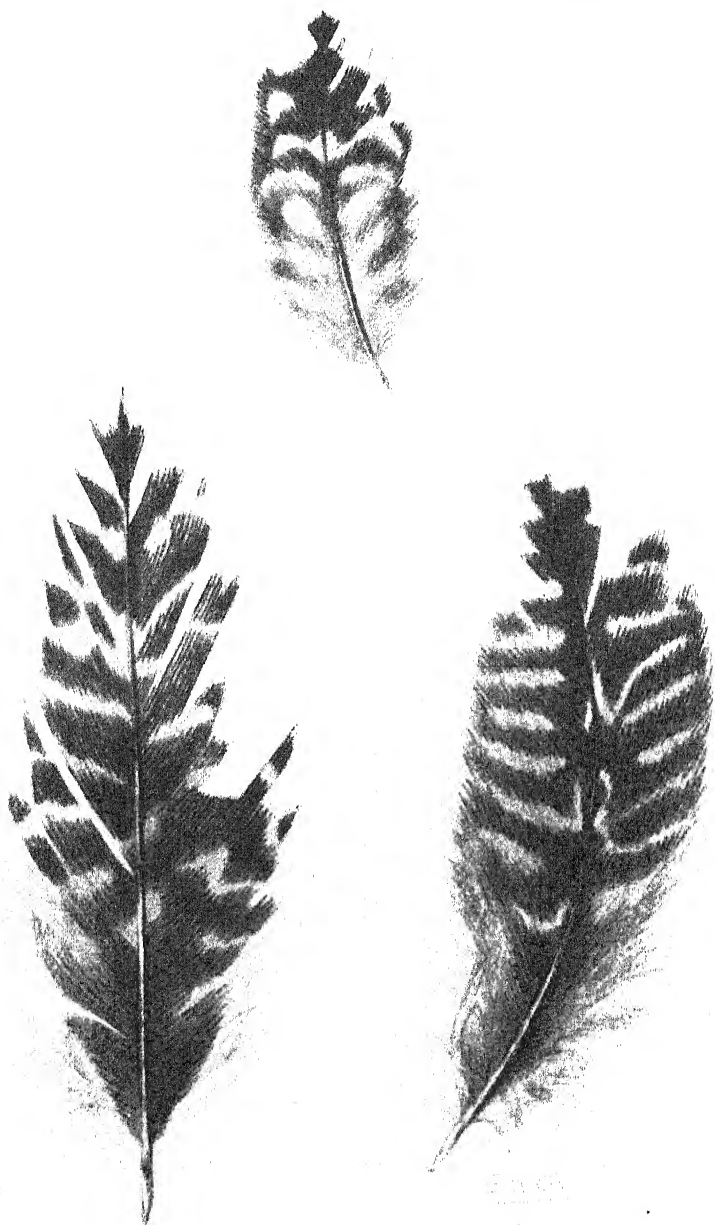


Andre & Seigh, Ltd.

FEMALE GROUSE, RED TYPE ; FEATHERS FROM FLANKS.





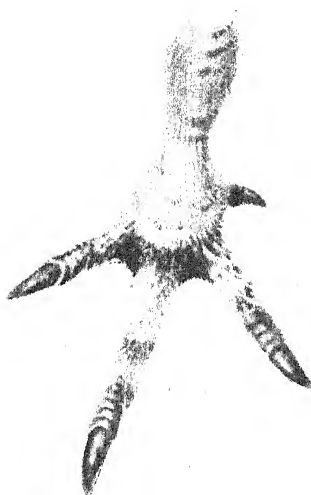


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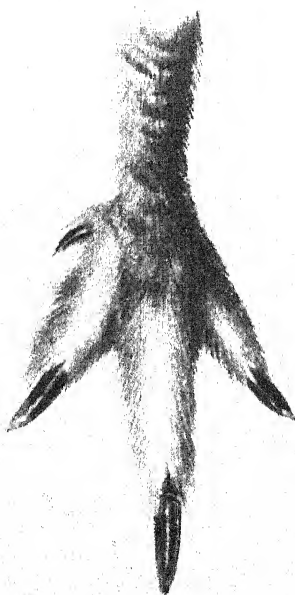
FEMALE GROUSE, RED TYPE ; WORN UPPER TAIL-COVERTS.



1



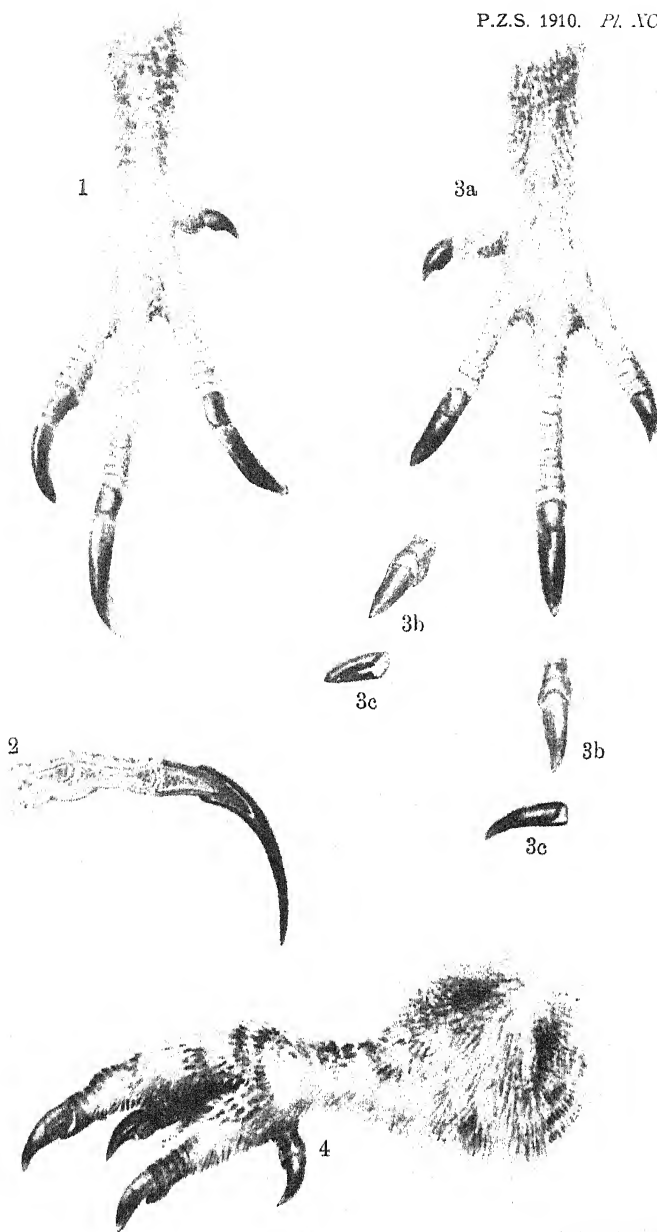
2



Andre & Seigh, Ltd.

FEET OF RED GROUSE : (1) NEW WINTER-FEATHERS AND NAILS ;  
(2) FULL WINTER-PLUMAGE.



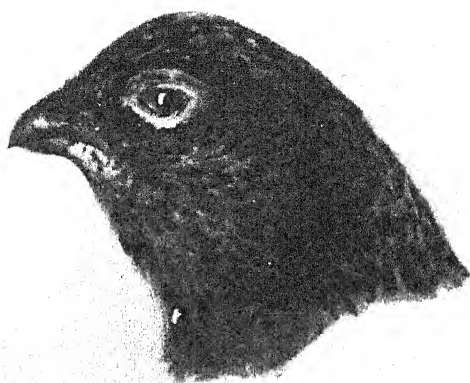


Andre & Steigh, Ltd.

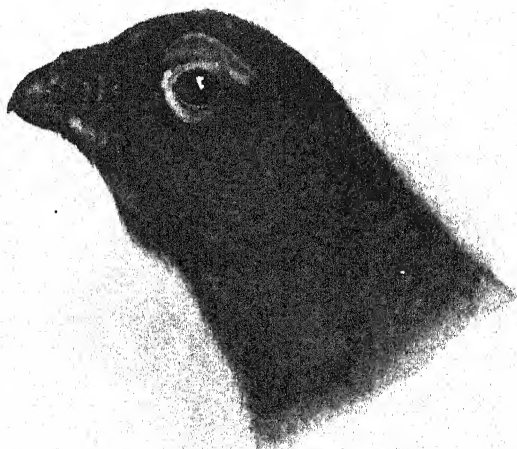
FEET OF GROUSE SHOWING STAGES IN MOULTING OF NAILS.



1



2



Andre & Sleigh, Ltd.

HEADS OF GROUSE : (1) FEMALE ; (2) MALE.





1



2



3



HEADS OF : (1) FEMALE GROUSE ; (2) MALE GROUSE ; AND  
(3) PTARMIGAN, SHOWING SUPRA-ORBITAL COMBS.

Andre & Steigh, Ltd.

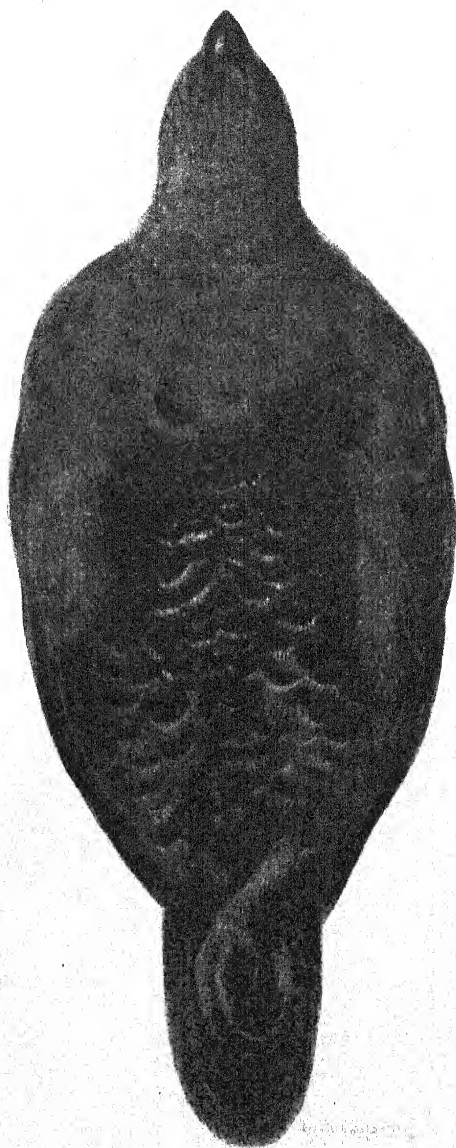




Andre & Sleigh, Ltd.

HEAD OF BLACKCOCK. SHOWING SUPRA-ORBITAL COMB.

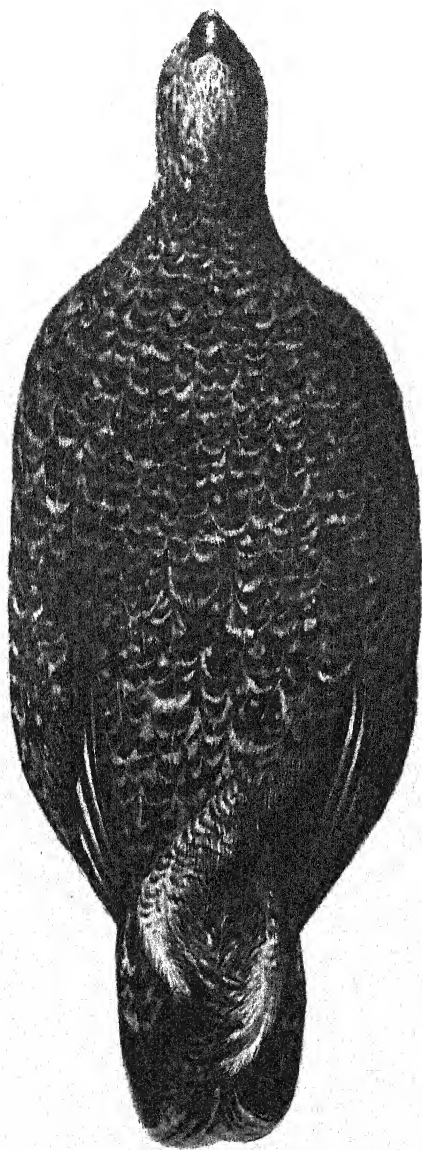




Andre & Seigh, Ltd.

MALE GROUSE SHOWING ABNORMAL ERYTHRISM.



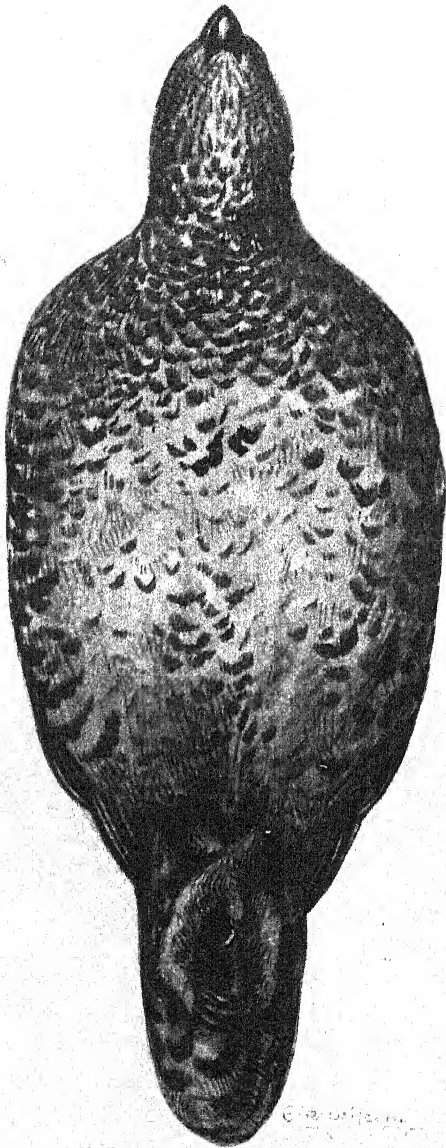


Andre & Stiegh, Ltd.

FEMALE GROUSE, BUFF-BARRED TYPE.







Andre & Sleigh, Ltd.

FEMALE GROUSE, ABNORMAL YELLOW VARIETY.

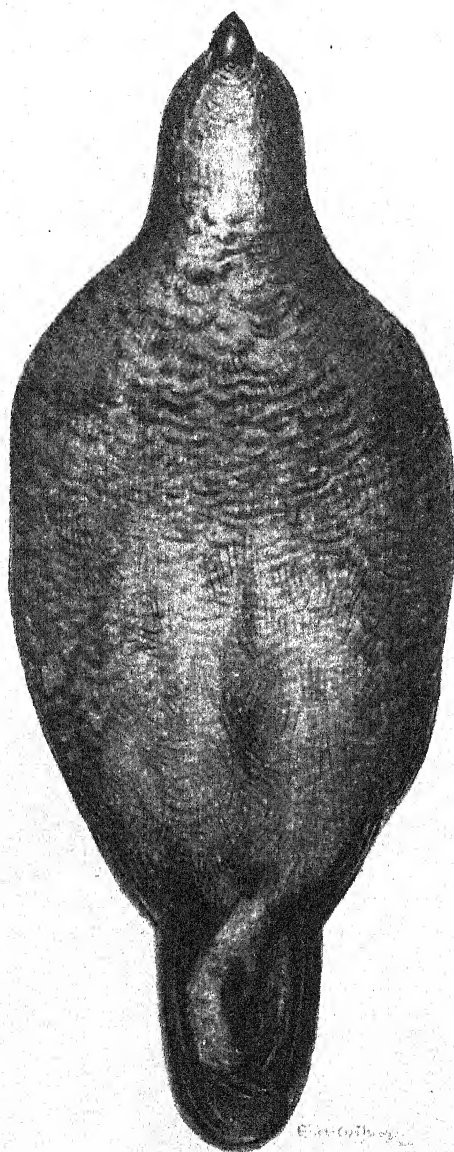




Andre & Siegh, Ltd

FEMALE GROUSE, GREY VARIETY.





Emm. G. Th. 1910.

Andre & Siegh, Ltd.

**FEMALE GROUSE, GREY VARIETY.**

(Type of *L. persicus*, G. R. GRAY.)



vexed question of moult and plumage-changes in the Red Grouse, and their proper interpretation.

Without referring in detail to the points upon which differences of opinion have before now arisen, it may be shown that much misunderstanding upon such a difficult subject as this is based upon a different rendering of facts into words, facts which were recognized and perfectly well explained by Mr. Ogilvie-Grant in 1893. Both he and Mr. Millais have made the subject of plumage-changes in the game-birds, and especially in the Grouse, a special study, and it must be admitted that there are very few points upon which they have touched which seem to require further explanation; and still fewer points, if any, which can be brought to light for the first time in connection with the plumage-changes of the Red Grouse. A monograph on the Red Grouse, such as the Report of the Grouse Disease Inquiry, would, however, be obviously incomplete without an account of the plumage-changes of the bird itself; and it so happens that during the past six years of the Grouse Disease Inquiry's existence the collection of some six hundred Red Grouse skins, representing every age, phase and change of plumage in that bird, has given a unique opportunity for an independent revision of the work already done—an opportunity such as has never occurred before in the study of any single species of British bird for observing the effect of disease upon moult and feather-growth. So it happens that although the work as it stands has been so nearly completed by the labours of the two ornithologists already mentioned, there are still points of interest to which attention may be drawn, especially in connection with the marked effect which parasitism and other wasting diseases have upon the moult and growth of feathers; and it is to this influence of disease that attention will be particularly drawn in the present paper.

It is almost incredible that a moult should be deferred from one season to another or even to a third, and that the right plumage should eventually be produced if the bird by means of good food and good weather is at last enabled to recover its health and grow any new feathers at all. It is interesting and to some people, such as sportsmen and gamekeepers, even useful to know that bare featherless legs and feet, which have so long been considered a sure sign of disease in the Red Grouse, may, in certain months of the year, be an unavoidable accompaniment of really good health, while thickly feathered legs in the same month are a sure sign of deferred moult and of sickness. It is only when the proper season for the moult of the leg and foot-feathering is completely understood, that we can begin to understand the reason for attaching an unfavourable prognosis to heavy leg-feathering when the legs should have been featherless, and an equally favourable prognosis to bare legs when the legs should certainly have been bare (Pls. XCII. & XCIII.).

To return, however, to the two plumages of the healthy cock Grouse. They are distinguished by Mr. Ogilvie-Grant as the



*autumn-plumage* and the *winter-summer-plumage*, and he says further that the cock "has no distinct summer-plumage." It is perfectly easy to see what is meant by this, and also by the statement which follows, that the cock "retains the winter-plumage throughout the breeding-season."

Mr. Millais also, in speaking of the cock Grouse, makes use of the expression *autumn-plumage* which, he says, appears late in June; and he adds that the autumn-plumage together with the "*Spring feathers*" (or what Mr. Ogilvie-Grant considers the first beginning of the autumn-plumage on the Grouse's neck) remain till the main moult in August and September.

Mr. Millais also makes the following statement, which appears to be based on a misinterpretation. He says "as a matter of fact the male Grouse sheds in September and August a plumage which is a mixture of its Winter, Spring, and Eclipse feathers."

These so-called "Spring" and "Eclipse" feathers are no doubt, as Mr. Ogilvie-Grant holds, the commencement of the plumage, which is completed gradually during the summer months, and which he has described as the *autumn-plumage*. It is naturally a little misleading to find the autumn-plumage beginning to appear in early summer, but so long as the term is understood to mean the paler, more buff-coloured plumage with bolder bars of black, which begins to appear first on the neck of the cock at the end of May or early in June and is eventually cast for the winter-plumage in October, there need be no real misunderstanding.

That feathers of the previous winter-plumage should be mentioned in speaking of the *moult* of this autumn-plumage is also quite intelligible, since the old winter-plumage of the breast and abdomen is being quickly shed and replaced by a similar new winter-plumage at the time when the autumn-plumage on the rest of the body is being cast. There are in addition very frequently a few feathers of the copper-red plumage on the chin really belonging to and remaining over from the previous winter-plumage.

Instead of going into further details, however, with regard to the two moults and plumages of the cock Grouse, it will be simpler at this point to take its plumage-changes in detail, successively month by month, explaining as nearly as possible what can be gathered from the examination of a series of skins such as has been brought together by the Committee of Inquiry, including as it does a great number of specimens in all stages of disease as well as in health.

They illustrate every month of the year and most of the local variations to be found in England, Scotland, and Ireland; and there are a sufficient number of sick as well as healthy birds to show the very great influence of disease in altering the capacity of the individual for feather-growth. Unless this effect, which results as a rule in the Red Grouse from excessive parasitism, is fully recognized there will always be misunderstandings upon the

moult of this bird, for almost every Grouse in the country is to some extent infested with parasitic worms, and there are years when irregularity of moult is the rule rather than the exception. Moreover, it so happens that in autumn, when birds are being shot in large numbers, the survivors of the worst two months of the year for Grouse-disease mortality, that is, the survivors of May and June, are all convalescing; but they are convalescing with their plumage-changes all retarded and put completely out of order and routine. In this way it is possible in September to kill two birds on the same day both of which have the chestnut-coloured feathers of the winter-plumage on the chin and throat; but upon examination it may be seen that in one bird the edges of these feathers are frayed and worn and the colour faded, showing that they have survived from the *previous* winter-plumage; whereas in the other bird they are hardly free of the scaly sheaths in which they grew, and are really precocious feathers of the *coming* winter-plumage. This is only one of the many traps which result from the deleterious influence which disease exerts upon a bird's capacity for feather-growth and replacement and so upon the regularity of its moult.

There is another point to which attention must be drawn before entering upon a systematic description of the monthly changes of feather in the cock Grouse. It is as to whether the autumn-plumage of the cock can be correctly described as an "Eclipse" plumage, comparable as it obviously is in character with the Spring breeding-plumage in the hen, but appearing just two months later and after the breeding-season. In each sex the general change from winter to summer may be described as a change from a more richly pigmented, darker, black and chestnut, or rufous-chestnut plumage with rather fine transverse black markings, sometimes almost vermiculate in character, to a less-richly pigmented, paler, buff or rufous-buff or tawny-buff plumage with characteristically broad black bars and transverse markings.

To each sex, moreover, the characteristic buff and black broad-banded summer-plumage is given its special appearance on the dorsal aspect by the growth of feathers with large black centres and a few buff or tawny-buff subterminal bars of considerable width and a terminal border or spot of the palest buff, which is a very conspicuous feature on the back of most hens, and often only less conspicuous in the cock. In the cock, however, this plumage appears just two months later, and is less beautifully developed than in the hen.

There is without doubt a general broad resemblance first between the cock and the hen Grouse when the former is in its "winter-plumage" and the latter in its "autumn-plumage"; and, secondly, between the cock and the hen Grouse when the former is in its "autumn-plumage" and the latter in its "spring-plumage."

The perplexing fact is that these general resemblances are not synchronous in the two sexes, a peculiarity first discovered by

Mr. Ogilvie-Grant, for, as already pointed out, there is an interval of two months between the moults of the cock and hen.

Again, it might reasonably be expected that, as the Ptarmigan and the Scandinavian Willow-Grouse have not two plumages in the year, but three, some suggestion of the third plumage might be forthcoming in the Red Grouse. But the Red Grouse has only two moults. Mr. Ogilvie-Grant, however, explains the position by saying that the buff and black plumage of the hen answers to the spring-plumage of the hen Ptarmigan, while the buff and black plumage of the cock Grouse answers to the autumn-plumage of the cock Ptarmigan. The grounds for this position will be considered later in the light of the possible effect which continued disease may have in permanently altering the season of a moult.

Beginning now with the cock Red Grouse in *January*, and taking its appearance from the ventral aspect first, the uniformity of the series is a very conspicuous feature. Every healthy bird is chestnut or rufous-chestnut and black, with fine, almost vermiculate black cross-lines over it.

Even in the blackest birds the throat and fore-neck are always of a rich copper-red colour with very little or no black edging at the borders of the feathers, which are usually barred with black only on the actual chin. Here there may be also more or less of white tippings, even to the formation of two white moustachios leading downwards from the gape, sometimes an inch in length. This may be a feature either of the black type or of the red \* (Pls. LXXIX. & LXXX.). In some very red and black Red Grouse the abdominal feathers are also freely and broadly tipped with white; and this may sometimes be seen even on the feathers of the upperparts (Pl. LXXXI.). The legs and feet are thickly feathered, and are white, or white with brownish barring. The claws are often in this month very long and strong.

Occasionally a pale bleached feather of the preceding "autumn-plumage" is to be found on the flanks, middle of the breast or neck, and may be recognized by its frayed edges; and occasionally (*e. g.* No. 539), in a very backward bird, there may be many such worn and faded feathers on the chest and flanks, but such a case is invariably the result of sickness.

On the dorsal side there is again, broadly speaking, a general uniformity of chestnut, bright or dark, or of blackish feathers, with fine black transverse markings; but in almost every bird there may be found a considerable number of the old black-centred "autumn-plumage" feathers remaining, with their frayed and faded edges of whitish-buff (Pl. LXXXII.). On the lower back and rump the more worn and faded feathers predominate.

The primary and secondary quills are all complete and are but a

\* The whole paper deals with the Red Grouse (*Lagopus scoticus* Lath.). The terms "black Red Grouse" and "buff-spotted or white-spotted Red Grouse" must not be confused with similar terms for other species of Grouse.

few months old, having been renewed between June and August and the same may be said of the rectrices.

The following points in the cock Grouse of January are characteristic :—

1. The rich copper-red, generally unbarred feathers of the throat and fore-neck (Pl. XCIV. fig. 2).
2. The fine barring of the chestnut, dark rufous-chestnut, or blackish-brown of the back, with the scattered black-centred feathers of the last "autumn-plumage."
3. The thick white feathering of the feet and legs, which soon becomes blackened and worn by the "burrens" or "colons," the charred stalks of old burnt heather.
4. The perfect flight-feathers of the wings and tail.
5. The enormous claws.

In *February* the cock Grouse is still in the darker winter-plumage.

Young, sheathed and growing broad-barred feathers, the remains of the "winter-plumage," may still occasionally be found on the hind-neck, nape, and head in backward birds.

In *March* the cock Grouse normally shows no change; but towards the end of the month in exceptional instances individual birds may be found with a few precocious feathers of the autumn-plumage making their appearance on the back of the head and neck. These are very probably feathers irregularly acquired to take the place of those which have been lost during encounters with other males.

In *April* the cock Grouse still shows no change whatever.

In this month there are often greatly increased opportunities for the addition of skins to a collection, because it happens to be a month of very high mortality from "disease." The birds are found and can be collected not only by the keepers who are out early in the month in search of fox-earths, and who are generally also burning heather, but also, later on, by the shepherds, who are constantly ranging the moor in the lambing time.

The result during the last five years has been a great accession of Grouse-skins to the Inquiry's collection, in March, with a very large proportion of males badly diseased, and fewer birds in perfect health. Therefore in the series of skins of cock-birds representing April, the great majority are very backward. Healthy birds have still the old rich red copper-coloured throat of the winter-plumage, and fresh-looking "autumn" feathers round the neck, upper-back and mantle, while the winter and old autumn-plumage of the rump and back is bleached and faded. The backward birds are easily picked out, as they have not yet assumed their "winter" plumage, and are still mostly clad in old worn autumn-plumage of the previous year.

It is important to note the extraordinary discrepancies which so commonly occur in the plumage of the Red Grouse owing to disease, whereby the deferred moult becomes in some years almost

the rule, and the rule of health becomes almost the exception. It is a very difficult matter, indeed, for anyone who has not had the opportunity of examining an extensive series of Grouse-skins, in disease as well as in health, and covering every month of the year, to come to any true conclusion about the moult. Diseased conditions often entirely mask the normal plumage-changes from time to time, and it is far more important to realise this than to examine thousands of more or less healthy birds shot in the ordinary course of events in the shooting-season. A study of abnormal plumage-changes in diseased Grouse is essential if the discrepancies which arise in the moult of what are often wrongly considered normal birds are ever to be explained. Once this point is grasped the question becomes much simpler; and it is because the Grouse Disease Committee has had such a unique opportunity for studying both sides of the question that it has been deemed necessary to enter into these plumage-changes at such length.

The legs and feet of a healthy bird in *April* should be getting worn and thinly feathered. If a bird has newly and thickly-feathered legs and feet, it means, almost certainly, that the "winter" plumage has been put on very late. The healthy Grouse should now be moulting the feathers of the feet and legs, so that bareness or lack of feathers becomes in them a sign of health in April and thickly-feathered legs a sign of sickness; this is the precise contrary of what has almost become proverbial on the moor, that bare legs indicate disease; though for the later autumn months the saying is quite true.

In *May* the preponderance of cock birds found dead, and therefore of skins of cock birds in the May collection showing belated moult, is again a large one. The healthy cock is still in his much-worn winter-plumage, but on the head and neck some feathers of the new autumn-plumage are beginning to make their appearance (Pls. LXXXIII. & LXXXIV.).

In *June* the disease mortality, due to Strongylosis, is, as a rule, coming to an end. This at least is true for the adults, but for the young chicks June and July are often fatal months owing to Coccidiosis. Late in June the healthy cock Grouse can at last be said to have changed into his complete "autumn-plumage." The winter-plumage persists only on the abdomen and lower breast, on the actual chin which is blackish, with a few white spots, and on the throat, where a few red feathers still remain. The moulting of the quills and tail-feathers commences towards the end of the month. The rump and back are now completely covered with new black-centred feathers carrying broad-barred buff and black bands and a few have a whitish terminal spot, similar to that found in the female.

The head and neck, breast and throat, are now clothed with broad-barred buff and black feathers, quite distinct from the more chestnut and more finely black-marked plumage of the winter. It is impossible, in seeing a series of the birds showing this dis-

tinctive change, to avoid noticing how closely it approximates to the nesting-plumage of the hen, and yet to think and to speak of this "autumn" plumage as an "Eclipse" plumage. In every respect it closely resembles the breeding-plumage of the hen, and the one prominent discrepancy is that it has arrived in the cock just two months later than it is normally due in the hen, far too late to be a breeding-plumage.

It appears almost as though the pathological postponement of the moult, which is, after all, nothing but a sign and a symptom of disease, has gradually developed into a normal habit in the life of the bird; and one is led to think that this habitual disability in the cock Grouse, which results from *Strongylosis* during the nesting, courting, and breeding-season (a disability which causes the death of about eight cocks to every hen in April and in May), may have caused the alteration in the season of the moult, simply because the *vis vite* of the cock bird, insufficient as we now know it to be at the close of winter for the ordinary calls of reproduction, would be still more disastrously insufficient if preceded by an early moult.

At the present time the cock undoubtedly breeds in the winter-plumage, without any further acquisition of new feathers, and, as has recently been pointed out by Mr. Ogilvie-Grant, what have been regarded as new "spring-feathers" on the neck by Mr. Millais are in fact the *old* autumn-feathers, which on that part of the body do not become worn and faded.

That any feather of the Grouse, either in the cock or in the hen, was ever altered as to its pigment either in pattern, or in tone, or in any other character, when once it had completed growth and had been cut off from the circulation, is at present an assumption which is not well supported by the physiology of feather-growth.

Metchnikoff's observation upon the migration of leucocytes into hair and their action in removing pigment cannot for one moment be adduced as conclusive proof that the same thing may happen in the case of a full-grown feather. While the circulation is active in the feather-shaft, and for as long and in so far as it continues, pigmentation may be altered, and so may growth; but once allow, first that the circulation has ceased beyond the entrance to the base of the shaft, and secondly that the feather, although still attached to the epidermis, is cut off from the circulation in the deeper living layer of the skin, then the feather is no more likely or able to change the pigment which is responsible for its pattern or its colour (except by external means such as bleaching by sunlight) than if the same feather had been plucked out and kept entirely separate from the bird.

Once the feather is full-grown and the circulation in it stopped there is no reason to believe that any thing can alter it save sunlight and water, and oil supplied as an external unguent from the oil-gland. That *appearances* are most deceptive in this respect must be allowed. Feathers may be collected from

the flanks of hen Grouse which show every possible graduation between the perfect winter-plumage, almost vermiculate, flank-feather and the broad-barred, breeding-season, flank-feather of the summer hen. But it is very much more probable that the growing period of these ambiguous or intermediate feathers is one of great susceptibility to outside conditions, as we know the case to be in respect of the metabolic processes which are taking place within the hen-bird at the time. These are known to be exceedingly sensitive. Pigment is indisputably a product of tissue metabolism. It is often probably a mere waste product, but it appears at times to serve a special function notwithstanding. It is also certain that pigment is a production whose appearance, or failure to appear, is open to considerable vicissitudes in consequence of small recognized changes in physiological condition, and many less easily recognized changes in the general-metabolism of the body.

In the hen Grouse during the breeding-season pigment production is very actively at work, for we know that a very large amount is being produced for excretion in the pigment-glands of the lower part of the oviduct. This pigment, moreover, is precisely of the shade and colour which is characteristic not of the breeding-plumage, but of the winter dress of the hen and the cock Red Grouse. It is deposited in abundance normally on every egg, but it may also abnormally fail to be deposited or even produced at all, not only for the eggs in the oviduct, but in the circulating blood of the bird's whole system. Thus the feathers instead of becoming buff or brown, reddish or even black as they proceed in growth, may be any intermediate paler shade of buff, or even white, a character which is due generally to the complete absence of all pigment granules. The place of the pigment in such feathers is probably taken by shining air-globules, as it is in the hair and feathers of the majority of white animals and birds.

It is therefore easier to believe the suggestion that a sudden check, either by a change of temperature, or by wet and cold, or by want of sunshine, or by change in food, has for the time being so far affected the tissue metabolism of the bird that a feather which began to grow upon a circulation lacking pigment particles, or the waste products which produce them, and which was therefore originally planned for the paler plumage, may, by a sudden increase in the metabolism of the bird and so in the output of waste products to the blood, be completed as a feather of the more deeply pigmented plumage, thus producing a feather with the characters of both.

This is a plausible explanation, but is still open to some doubt, for the difference between the broad-banded buff and black flank-feather of the nesting hen, and the dark red-brown finely cross-lined feather of the same bird in winter, is obviously greater as regards pigment distribution than as regards the actual quantity of pigment deposited in the feathers.

If there are, as has been held, distinct pigments, such, for example, as buff, black, and orange-red, in the various colour-tones of the Red Grouse, it becomes easier to see that the loss of the red pigment which is utilized for the eggs, leaves the buff and the black in greater quantity for the nesting-season plumage. In the winter all three would once more be available.

The fat of the nesting hen is distinctly rich in colour, but in no case that we have seen has it resembled the orange-coloured fat which is often seen in overfed Pheasants, and quite commonly in Gulls and Terns which have been feeding on red crustaceans. In these birds the orange-red fat or oil, tints not merely the buff beneath the skin, but the white feathers of the breast and body which often present a beautiful rosy flush.

The whole question of pigment production and pigment distribution, intimately connected as it is with the question of the excretion of waste products and the deposition of fat both in health and in disease, has not reached a stage which admits of dogmatic statement upon the subject of pattern change in feathers without moult.

One recognized method of changing a colour-pattern in feathers without moult is to be seen in the male of the familiar House Sparrow, which produces a handsome jet-black cravat in the breeding-season, where before was a nondescript greyish throat; and this it does by the simple process of shedding the grey ends of the feathers, leaving the blacker parts exposed. This method is common among birds, but the Red Grouse has been credited with changing *in situ* the colour and pattern of the flank-feathers. Now, with still less reason as it seems, the cock bird has been credited by Mr. Millais with achieving his summer or breeding-plumage "for the most part by repigmentation and pattern change of most of the winter-feathers below the neck."

This view cannot be upheld physiologically, and there is much to uphold the contention that the feathers which are believed to effect this change of pattern without moult, are actually new growing feathers. This can readily be shown by the demonstration of their unshed sheaths. The misleading birds are again in this case the cocks which have been too sick to shed the previous "autumn-plumage," and so are still struggling, and with increasing success as the food improves, to produce a "winter-plumage," which they should and would, in health, have achieved in October.

That the cock bird should moult the feathers of the legs and feet between March 30th and June 17th is no longer difficult to understand when the prevalence of Strongylosis is fully grasped. No bird is safe from the Nematode infestation, and one is led to think that the majority of cock birds are so badly infested that they are forced to defer the autumn-moult which should precede that of the previous winter. It is therefore obvious that between March and June there will be every stage of good or bad leg- and foot-feathering between the newly acquired thick white



winter-stocking of the sick cock, and the naked featherless clean moulted leg and foot of the really healthy male bird, in June. In July, again, will be found the healthy cock bird beginning to produce white feather-tips over the legs and feet.

In *July* the general appearance of the healthy cock is much lighter in colour-tone and much more broken and mottled in pattern-character than that of the same bird in the winter. The claws are in many cases now ready to be shed, and the primaries, secondaries and tail-feathers are in moult. Some six or eight new clean grown primaries are often to be found in July, and the long tail-coverts are broad-barred buff and black.

In *August* the cock Grouse has, of course, the appearance of full summer- or autumn-plumage, but it requires very little examination to see that he has already begun to put on feathers of the winter-plumage.

He now rapidly sheds the old feathers of the last winter's plumage which remained throughout the summer upon his breast and abdomen, and replaces them with the exceedingly handsome narrow cross-barred red or brown or blackish feathers of the coming winter-plumage.

There is no second moult or replacement of these feathers of the breast and abdomen in the cock. Once in the year is enough for this special area, and the feathers that carry through are wholly of the winter-plumage. They are often broadly tipped with white.

The chin-feathers which survived with those of the breast and abdomen are now also replaced by new ones. It is noticeable that in the Ptarmigan also it is the white feathering of the chin and of the breast and belly, as well as of the wings and tail, which is changed once only in the year, exactly as with the winter-plumage of the Grouse. It suggests that these two plumages are analogous in each.

The plumage-changes in the Ptarmigan are, strange to say, quite different to the changes in the Grouse. The Ptarmigan has three distinct moults and plumages in the year. The Red Grouse has but two.

In *August*, as has been said, the cock Red Grouse has begun to put on his winter-plumage. The feathers of the breast and abdomen are full of sheaths and sheath-scurf, the growth of these feathers being very rapid and often scarcely noticeable.

On the rump, back, and to a less extent on the shoulders, new rich red-brown feathers finely marked with black lines are showing here and there.

Primaries, secondaries, tail-feathers and coverts are now replaced by new and blackish feathers with perfect and unbroken outlines.

Even a few new rich copper-coloured feathers are appearing as isolated touches of bright colour amongst the faded broad-barred autumn-feathers of the upper breast.

The feet and legs are bare, save where new white feather-tips

are just appearing through the skin, and the claws of all the healthy birds are being shed.

In *September* the chin and throat of the cock Grouse are a mixture of many pale autumn-feathers much worn and faded, and a few new copper-red ones.

Most of the "autumn-plumage" feathers are now falling out, more or less frayed and faded.

The breast and abdomen, wings and tail are now clothed with altogether new feathers, while the head and neck, back, shoulders, rump, and coverts of the tail are in a transition state, the "autumn" feathers contrasting with the new rich chestnut and darker brownish winter-feathers with their fine black transverse markings.

The feathers of the legs and feet of healthy birds are rapidly growing to form thick white stockings for the winter. Bare legs in *September* are a sign of belated moult or, in other words, a sign of sickness.

In *October*, for the first time since the preceding winter, the red and black varieties of Red Grouse become once more conspicuously distinct. This result is due to the new growth of fully pigmented feathers, either red or black, upon the under surface of the body.

The upper neck is rapidly becoming copper-red. The chin and throat still show a proportion of the faded buff "autumn" feathers among the red, the former looking spotty and pale.

On the back the new chestnut and black feathers are rapidly replacing the faded autumn-feathers.

Some perfectly healthy cocks still look as if in "autumn-plumage," while others, on the contrary, have nearly completed their winter dress.

The legs and feet are thickly covered with white feathers, and the nails are uniformly small, as the old claws have all been shed. Their growth, however, is extremely rapid.

In *November* the cock Grouse drops most of the remaining "autumn-plumage." By the end of the month his moult is complete, but on the neck and back a greater or lesser number of these feathers are retained till the following summer.

The most striking characteristics of the winter-plumage are the rich copper-coloured neck and throat, and, in the darker varieties which are common in the Scottish Highlands, the contrasting blackness of the upper breast and abdomen, often broadly flecked with pure white tips.

Amongst the cocks there are several well-defined and easily recognized varieties, which seem to have a certain regularity of distribution geographically. These will be found fully considered below.

It must not, however, be forgotten that owing to innumerable efforts, which have been more or less successfully made from time to time, to transfer Red Grouse from one part of the country to another, the distinction of local variations has become a thing

of the past and is now impossible except upon a very limited scale.

The attempt, however, can be made, and the number of specimens in the Committee's Collection of Red Grouse skins makes it possible to arrive at some conclusions.

## PART II.

### *Plumage Changes of the Hen Grouse.*

The two changes of plumage in the hen Grouse are completed, as has already been explained above, in the one case by the end of April or the beginning of May, and in the other case by July and August.

The actual feather-changes in both cock and hen are really very comparable in character, notwithstanding the discrepancy as to season; and allowing for the difference of two months which makes the moult in the two sexes asynchronous, they may be described and explained in very much the same terms.

Mr. Ogilvie-Grant was the first to draw attention to the exceptional want of agreement in the seasons chosen by the two sexes of the Red Grouse for their moults, and as in the cock's plumage he makes use of the terms "autumn" and "winter-summer" or "winter" plumages, which have therefore been used here, so in speaking of the hen's plumages it will be well to adhere similarly to the expressions used by him, and to call them "summer" and "autumn-winter" or "autumn" plumages.

Exception may be taken, and indeed has been taken, to these names, as being inappropriate and inexact, but they are sufficiently exact for all practical purposes, and so long as moults and plumage-changes are not completed in a week but are spread over a period of several months, so long will there be some inexactitude in the terminology of these moults and plumages if they are named according to the months or seasons. It is immaterial so long as the term is sufficiently defined, for it is obviously impossible to use a term so exact as to require no definition.

The hen Grouse moults twice in the year, and wears her "summer-plumage" as the breeding-dress from April to July, and her "autumn" or "autumn to winter" plumage from August to March.

These changes may be expressed in terms of comparison with the cock, as a case of plumage change in which the hen has two annual moults, exactly as has the cock, but both moults occur two months earlier in the hen than in the cock.

The hen's "summer" or breeding-plumage is a very beautiful dress, variable to a considerable extent it is true, but yet having a general uniformity which becomes the more obvious as a greater series of skins in any particular phase of plumage is examined.

Opportunities for even seeing the hen Grouse, to say nothing of obtaining her skin, in the full breeding-plumage are rare; and thus it has fallen out that in even the large series of Grouse

skins at South Kensington and at Cambridge, for example, this phase is somewhat poorly represented.

The Grouse Inquiry Committee has been to some extent more fortunate and has obtained a great many skins of hens in the summer-plumage (see schedule of material, p. 1022), so that points of resemblance can be noted at sight and individual variations perforce take their proper and, as it turns out, rather less significant places. It has been a marked feature in the whole collection of 580 skins, that as the series grew and the general uniformity became more marked, the individual variations of which one was inclined to make much at first became gradually relegated to their subordinate position in the background.

Uniformity, albeit with endless minor variations, is the rule in the Grouse as it is in every other creature that leads an unprotected existence under natural conditions. How long it will continue in the protected, often over-protected, Grouse, remains to be seen. It is possible that such variations as already occur are to some extent a modern development, but on this point there is at present insufficient evidence to amount to certainty.

Beginning once more with *January*, and considering the changes of plumage from month to month in the hen Grouse, it may be said that some hens when examined on the under side are hardly distinguishable in this month by their plumage from some cocks. On the dorsum it is different, and a healthy hen in January is unmistakable owing to the terminal spots of buff which appear almost invariably, though occasionally in limited numbers, on the feathers of the back.

In some healthy hens the chin is sometimes still pale buff in colour, owing to the persistence of summer-plumage feathers of the preceding year. The throat and fore-neck, on the other hand, are copper-red, but rarely so uniformly red as in the cock (Pl. XCIV.).

The copper-red feathers seem to begin on the fore-neck and proceed towards the chin, so that the chin often remains buff and black when the throat is already red.

Except in very backward birds, which have been sick, the old and faded broad-barred feathers of the flanks are never found in January. The legs and feet are white and thickly feathered and the claws are long and strong.

In *February* the bird is still in the same plumage as in January. In a few forward birds the feathers of the summer-dress are beginning to make their appearance on the back of the neck about the middle of the month.

In *March*, the change from autumn-plumage to spring breeding-plumage is, in healthy birds, now quite unmistakable, though many birds are very backward owing to disease. All doubt as to the sex, whether from above or below, is now removed except in cases of disease.

The broad-barred buff and black feathers of the flanks are now appearing and are most conspicuous and characteristic, while the

whole of the lower breast and abdomen covered by the red-brown or red-black finely barred feathers of September growth are still in excellent condition and remain unchanged.

The chin, throat, neck, and upper breast are now mixed with broad-barred black and yellow feathers in forward birds; while in backward birds the throat and fore-neck may still be clad in copper-red feathers.

The legs and feet are already looking worn and less well-feathered, but the claws are long.

In *April* and in *May*, for the simple reason that many hen Grouse died of Grouse Disease during the past six years of the Inquiry's work, the proportion of skins of backward hens is large.

The birds thus picked up dead carry one immediately back again to winter, for although they ought by this time to be putting the finishing touches to their spring-plumage, they are, in fact, but just succeeding in the belated effort to put on the autumn-dress. They are thus a clear six months late, and afford the most misleading seasonal characters imaginable. Their legs and feet, instead of being worn and almost moulted clean, are at last, after a winter spent with almost naked legs, well-clothed with thick white feathers. The appearance of the legs therefore in the hens, as in the cocks, is totally misleading to the Keeper or to the Sportsman who considers bare unfeathered legs to be a sign of Grouse Disease. It holds good for autumn only, and in spring precisely the opposite is the case, for in April, May, and June none but healthy birds have naked legs and feet.

The general character of advanced and healthy birds towards the end of April and in May is that of a complete spring-plumage. The whole of the upperparts are broadly barred with buff and black, and marked with conspicuous terminal whitish-buff spots or bars. The underparts, again, are broadly barred with buff and black, from the chin to the throat and neck, over the breast and down the flanks, while the central lower breast and abdomen are still in the autumn-plumage of the previous September (Pls. LXXXVI.-LXXXVIII.).

White terminal spots may, of course, be present on the breast and abdomen. These are a local or an individual character which will be mentioned later in dealing with varieties of feather-pattern and coloration.

The flank-feathers of the hen in the full spring-plumage show much diversity of pattern. This same diversity even in the same individual bird has led to the belief that the pattern may be changed in an unmoulted feather from the autumn-plumage arrangement of red-brown and reddish-black finely barred with lines of black to a much bolder barring of buff and black. It has been surmised, from the examination of single feathers, that the change commences in the centre of the feather on either side of the shaft, and gradually produces another pattern of a totally different colour. But can this be possible

in a feather which has long been fully grown, and which has presumably been long cut off from any blood or lymph supply and which is as dead as if it had been shed? (Pl. XC.)

It is almost certain that rearrangement of the pigment or of the pattern in this way is quite out of the question, and the reasons for so thinking have already been discussed.

The legs and feet of the hen Grouse in April and in May are very poorly feathered and the claws are very long (Pls. XCII., XCIII.).

In June the legs and feet are almost bare, and the claws begin to drop off. The precise date of this shedding of the claws is again really a part of the moult, and is, in consequence, equally dependent upon the health of the bird. Sick birds which have survived the spring mortality are always late in the shedding of their claws, and equally late in the changing of their feathers. The claws are shed, both in health and in disease, but once a year, and the casting is synchronous as a rule with the disappearance of the autumn-dress. The figures (Pl. XCIII.) by which this process is illustrated require but little explanation. The whole of the year's growth of horny black nail becomes loose on the soft and growing vascular matrix, and when quite ready to be cast can be easily pulled off like a little cap. The young nail beneath is at first soft and pink and vascular and very short, but soon hardens and deepens in colour, and in a month or two has grown to be a useful nail of horn. The transverse or circular groove which is left at the point of detachment of the old nail is quite a useful indication of age in cases where there is a doubt as to a bird being over twelve months old or of the year. The presence of the groove showing that the claws have once at least been shed is conclusive proof that the bird is more than twelve months old.

In June there is another characteristic appearance in the hens, namely the bare patch of abdominal skin which results from the shedding of the abdominal feathers, grown in the previous September. The loss of these feathers leaves a naked patch of skin on the abdomen of a hen that has been sitting, and this patch remains naked for the next few months.

The general character of a June hen in health is that of the completed summer-nestling plumage, broad-barred buff and black over all the upper- and underparts, excepting the abdominal area, the lower breast, wings and tail. But it looks already somewhat faded and worn; and it is quite probable that in acquiring so perfect a plumage for sitting unnoticed on a nest built amongst the heather, the economic absence of the redder pigment in the feathers is in part a result of the acknowledged fact that for longer and more trying use and for wear and tear in feathers, darker pigments are required, whereas for the short-lived and less exacting requirements of the summer-plumage in the Grouse from April to June the buff and black feathers, with very much poorer wearing qualities, are found to be sufficient.

The accompanying figures of a few worn-out and moulting feathers taken from a hen in summer-plumage, show how distinctly better the black pigmented parts of the feather stand wear and tear than the yellow parts (Pl. XCI.). Certain pigments have a value, therefore, of a very practical nature apart altogether from the more æsthetic point of view of attractiveness or the often rather hypothetical view of assimilation to surroundings for purposes of safety or to assist in obtaining food. He would be unwise, however, who denied that all three views may be reasonably held to account for the very beautiful nesting-plumage of the hen Grouse.

It very occasionally happens that the hen Grouse, instead of retaining the redder plumage of the previous autumn's growth on the abdomen until it drops off during incubation, grows an almost universal spring-plumage of buff and black broad-barred feathers covering the lower breast and abdomen as well as the remainder of the body from head to tail. A skin showing this condition is preserved in the National Collection, and there is an almost equally perfect specimen in the Grouse Disease Inquiry's Collection, No. 919.

The more usual procedure is that the abdominal patch of autumnal plumage is lost during incubation and is then quickly replaced by a renewal of the autumnal feathers when the spring-plumage is also being shed. There remains, however, in the majority of birds a very quaint growth of belated spring-plumage, consisting of buff and black-barred feathers in two lines down each side of the centre of the naked patch, as though, for some occult reason, the intention to grow "spring-plumage" feathers upon this area had never been altogether lost. This peculiar persistence of belated intention shows itself as a patch of yellow feathers made up of the two linear areas of feather-growth in the midst of a much broader area of the autumn red-pigmented feathers which one would expect to find all over the abdomen (Pl. LXXXIX.).

It is conceivable that a small persistent remnant such as this, having no obvious connection with the surrounding plumage at the time or with the habits of the bird, or with the seasons, may yet have something to do with the third or lost "Eclipse" plumage which is still to be found in the grey plumage of the Ptarmigan, but is almost completely lost in the case of the Red Grouse.

In *July* the summer-plumage of healthy hens is much worn out, frayed at the edges and very definitely faded, and the feathers are already dropping out. On the chin, throat, and fore-neck new red feathers of the autumn-plumage looking rich and dark are already making their appearance. The back is as it was, but faded, and the flanks are still conspicuously broad-barred with buff and black; but the abdominal bare patch is now growing new autumn-plumage feathers with great rapidity from the centre outwards.

The primaries and secondaries have now commenced to moult.

There may be in July, in the hen, as many as six or eight old primaries in each wing with frayed tips, still to be renewed.

Precocious young birds of the year can readily be distinguished in July from hens in moult, because in the former the dark red-brown black-lined autumn-plumage is on the flanks, while the broad-barred buff and black, and rather worn-out chicken-feathers are in the centre of the abdomen. In the adult the distribution is reversed. The broad-barred buff and black feathers of the spring-plumage are on the flanks and the redder fine-barred autumn-plumage is appearing in the centre (compare Pl. XC. figs. *a*, *c*, *g*, *h*, *k*, & *n*, and fig. *d*).

In skin No. 284 there seems to be an unusual compromise in a very backward hen, owing to disease. The compromise is between the broad-barred and the winter-plumage with its very fine black cross-lines (Pl. XC. figs. *e*, *f*, *l*, & *m*).

The legs and feet in July are naked and the claws are very small; but the feathers are already showing through as small white points, not to be confused with broken shafts, which occasionally result from wear and tear in woody heather.

The plumage of the hen Grouse in August is well known. It has already been pointed out in another paragraph how, owing to the sudden increase of observation and owing to the sudden arrival of opportunities for examining an enormous number of birds over the whole country during this month, there has sprung up an idea that disease amongst Grouse has a recrudescence in the autumn. But this is not the case. There are probably fewer diseased birds on the moor in August than there are in July. In July, however, they are never seen, and therefore not suspected, but in August they are almost invariably shot and carefully picked out of every bag, and owing to the general interest in the question of disease, are almost always noticed, and in a large proportion of cases publicly notified.

Hence the idea that disease makes a new start in August and September.

As a matter of fact, however, these wasted birds are almost certainly convalescent. They have been diseased, and they are still suffering from disease, but thanks, in the majority of cases, to their sex (for the bulk of the sickly autumn birds are hens) they have avoided actual death in the two highest mortality months, April and May. Once tided over those fatal months the food and general conditions of life improve, the weight of the cock goes up and the balance is again in favour of recovery for him; and although with the hen the exigencies of incubation and the cares of the family continue to militate against her recovery until June and even to July, she then rapidly begins to put on weight, and in August and September has once more everything in her favour towards complete recovery.

Many sick-looking "piners" are shot upon the moors in August, but it should be remembered that in that month they are recovering from disease, not growing worse; and in September



many that were not up to the average weight the month before will now be practically normal and probably indistinguishable from healthy birds, were it not that their serious indisposition of the preceding months has put them behind their fellows in the matter of feather-change.

In *August*, therefore, the Committee's collection of skins contains a large number of examples of hen-birds showing deferred moult and belated growth of feather.

The normal healthy hen Grouse in August has already put off most of the broad-barred spring-plumage feathers of her nesting dress, and is very much like the cock-bird in appearance, with the same dark red-brown vermiculate or fine-barred plumage underneath, white-flecked or not, as the case may be, and above with a mixture of feathers new and old.

The legs and feet of a forward hen are already showing quite a fair growth of white feathers, and the nails have all been shed. The claws are therefore short and rather soft and the transverse sulcus or groove at the point of detachment is clearly marked.

In the wings there may still be a number of primaries to be changed.

In the convalescent "piner," on the other hand, the case is often very different.

She has still a most deplorably bleached and weathered breeding-plumage on her, with worn-out feathers, frayed or ragged, often with saw-toothed edges, showing the different effect of wear and tear on the pale buff-pigmented and black-pigmented parts.

The bird in this belated plumage has quite naked legs and feet and long unshed nails, or may at the most be just showing the points of a new growth of feathers through the skin; and in this state she is conspicuously shabby and ill to look upon in comparison with the splendid plumage recently acquired by her healthy sisters, and by the now almost universally healthy cocks.

But the point above all others to be remembered in this connection is that this hen is convalescent, and still has a couple of months of good food and good weather, as a rule, in which to complete her convalescence before the winter comes.

If the spring outbreak of disease has been severe—that is, if the general weather conditions of the preceding winter and early spring months have been such as to conduce to a heavy and widespread infestation of the grouse with the microscopic larval *trichostrongylus*—then both cocks and hens will be equally infested. But the breeding-season and the concomitant needs of the two sexes are, from April onwards, quite distinct.

The result of this is that there is often a large mortality of cocks in April and in May, and a much less marked mortality of hens, probably in the proportion of seven or eight cocks to one hen, but definitely occurring in the same two months.

There is no great mortality from strongylosis in any other months of the year. Yet, notwithstanding this, after May the cocks are suddenly relieved and rapidly recover, so that by August

there are almost no sick cocks; whereas, after May, the hens have still two very trying months to face, and although, thanks to the abundance of food, they probably most of them or nearly all of them succeed in struggling through, yet by August they have only just been relieved of their more pressing cares and disabilities, and so in August a very great number of them are still found to be in a very poor condition. The moment the disabilities are removed, however, they begin to recover, and it is this point which has so constantly been overlooked. Sick birds in August are convalescent, and however many there may be, it is not a sign of a new outbreak of disease, but a sign that the past spring infection was a heavy one, though less fatal than it might have been.

At the end of their own specially critical periods, the cocks have at any rate June, July, and August in which to pull themselves together by means of good food assisted by good weather; whereas the hens, at the end of *their* own specially critical period, have August and September. Hence the preponderance of sick-looking hens when the shooting begins, and the widespread, but erroneous, belief in a recrudescence of disease in autumn.

To return to the further consideration of the hen's change of plumage in *September*, her finest feature is now undoubtedly the clean new growth of bright red, or dark red or even black and white-flecked feathers of the breast and abdomen, with their narrow but even blacker markings.

The whole of this tract has now been shed, but is so quickly overgrown again that no bare skin is visible save in the middle area of the abdomen quite low down, where, as has been already pointed out, the new growth is of belated feathers coloured as in the spring-plumage, and therefore quite different to the rest around them.

There is still, as a rule, no access of new red feathers on the chin or throat of the healthy September hen, or at the most but a feather or two. But in the sick hen there is still often a sprinkling of the old red feathers of the preceding autumn-plumage, very faded, amongst the faded buff and black feathers of the belated spring-plumage.

On the back of even forward hens there is still a mixture of old and new plumage, and the scapulars are often faded to something like black and white, and are badly frayed at the ends.

The wings have now almost completed their moult, but there may still be a primary or two to change, even in very forward birds.

The legs and feet are rapidly becoming feathered for the winter, though in backward birds which have been sick they are still quite bare, and now, of course, this feature is quite truly to be taken as a sign of sickness and disease, though in a convalescing bird.

In *October* one may find a very backward bird with as many as three worn-out primaries in either wing to change; but, as a rule, the wing is perfect, the primaries and secondaries and their

coverts all completely new, and in the tail the rectrices are full-grown.

The legs and feet are now also fully feathered, though the thickness of the growth increases as the winter cold comes on.

On the back the bird now looks fresh and richly coloured, from head to tail, but a close search will always disclose a number of spring-plumage feathers which have still to be thrown off.

Beneath, the rich red-copper colour is gradually replacing all the previous buff on the chin and throat. The change hangs fire a little on the neck and upper breast, but it is still progressing. Whereas on the lower breast and belly the rich red or darker winter-plumage with its beautiful fine black cross-lines and pure white flecks is a very striking feature.

There are, in the Committee's collection of skins, a number of examples showing the result of disease in deferring the moult; many of these birds, even in October and November, have made no effort to get rid of the old, faded and completely worn-out spring-plumage. The majority of these birds have been so diseased in spring that they have not bred at all. The ovaries have throughout the season shown no development at all, and there are no signs, even in the earlier months, of the shedding or development of ova or of any increase in size of the oviduct. They have been true barren hens.

In some cases (*e. g.* in No. 1247) there are feathers of three separate plumages in November. There are the faded spring-plumage feathers of the current year, but mixed up with them here and there are new feathers of the autumn-plumage coming, and here and there exceedingly old worn feathers of the autumn-plumage of the year before.

No. 1225, an October hen, shows exceedingly well how the bare broody patch of the abdomen grows delayed broad-barred buff and black feathers, instead of the fine-barred darker autumn-plumage feathers which surround the patch. These broad-barred feathers appear in two parallel rows, breaking through the skin of the broody patch on either side of the median line; this growth is also well shown in a specimen at the British Museum of Natural History, which shows the point exceptionally well (Pl. LXXXIX.).

In *November* the chief alteration is the completion of the autumn-moult and the assumption of the autumn-plumage. The feathers of the upperparts have black middles, and are barred with rufous-chestnut and ornamented with the characteristic white or buff-coloured terminal spot.

In *December* the hen is in full autumn-winter plumage.

On the legs and feet she is well and thickly feathered; and on the under side, the chin and throat are dark red, as well as the fore-neck, and marked with broader black bars than upon the lower breast and abdomen, where the marking is of the finer type and the colour distinctly of the redder and darker autumn-plumage.

## PART III.

*Local Variation in the Plumage of the Red Grouse.*

The following notes are the outcome of an attempt to find some broad differences between Grouse from the Highlands and Lowlands, East Coast and West Coast, English, Welsh, and Irish moors.

It seemed possible that, with a large series of skins of a species peculiar to the British Isles and at the same time so variable, one might discover points in the coloration of the plumage or in the size of the birds which could be attributed to some of the varying physical conditions under which they live.

The artificial transportation of Grouse from one county to another, generally from the southern moors to the northern, often far removed from one another and with very different food and climate, has no doubt to some extent confused the issue. But this is a difficulty which will increase rather than decrease, and it is even possible that the purity of the British breed, at present the only species of bird peculiar to our Islands, may before long be entirely lost by the introduction of a foreign species on the mistaken supposition that the latter is free from the parasite of Grouse Disease. This is not the case, and even were it so the species has already been introduced here and there, and there has been some interbreeding with our own Red Grouse. There was at any rate some reason for thinking that, unless the opportunity for collecting a series of pure-bred British Red Grouse skins had been taken by the Committee, the same wide opportunity might not have occurred again before the introduction of foreign species had become popular.

The Grouse Inquiry's collection contains 580 skins of the Red Grouse, including 540 adult birds of both sexes and 40 chicks and pullets. These, however, cannot be taken all together in one series. It is essential, for purposes of comparison, that the male birds in their two plumages should be taken separately in two lots and the females in a similar manner. Therefore the skins have to be divided as follows:—

	No. of skins.			
Male birds in winter-plumage	...	...	...	241
Male birds in autumn-plumage	...	...	...	120
Female birds in autumn-plumage	...	...	...	108
Female birds in summer-plumage	...	...	...	71
Immature birds of the first 6 months	...	...	...	40

The largest series of skins is therefore that of the male birds in winter-plumage, and it so happens that this set, both as regards sex and plumage, is best adapted by its general uniformity to give some result when arranged map-wise over a large outline of Scotland and England.

The following is an analysis of the greater part of the collection of skins:—

	♂.		♀.		Totals.
	Jan. to May.	June to Dec.	Nov. to Apr.	May to Oct.	
Caithness .....	22	3	5	3	33
Sutherland .....	12	4	2	8	26
Ross .....	6	16	3	4	29
Inverness .....	30	14	5	8	57
Nairn .....	0	1	0	0	1
Moray .....	11	0	1	0	12
Banff .....	5	0	0	0	5
Aberdeen .....	3	3	0	3	9
Kincardine .....	2	0	2	0	4
Forfar .....	1	1	0	3	5
Perth .....	17	16	5	13	51
Argyll and Mull .....	19+1	5	0	9	34
Dumbarton .....	14	4	3	1	22
Stirling .....	1	3	0	4	8
Fife .....	1	0	0	0	1
Haddington .....	3	0	1	1	5
Midlothian .....	5	0	0	2	7
Lanark .....	1	1	0	1	3
Ayr .....	1	2	2	5	10
Arran .....	4	4	1	1	10
Peebles .....	2	1	0	0	3
Selkirk .....	7	4	0	4	15
Roxburgh .....	0	4	1	2	7
Dumfries .....	8	4	4	2	18
Kirkcudbright .....	5	3	1	0	9
Wigtown .....	0	1	0	3	4
Northumberland .....	9	1	4	2	16
Cumberland .....	1	0	0	4	5
Durham .....	0	0	1	0	1
Westmorland .....	8	1	2	1	12
Lancashire .....	2	1	1	0	4
Yorks .....	28	13	14	13	68
Derbyshire .....	1	0	0	1	2
Wales .....	10	0	3	0	13
Ireland .....	0	0	0	1	1
	240	110	61	99	510

Having thus sorted the skins into lots which are sufficiently uniform to allow of comparison, and having arranged one of these lots, the cocks in their winter-plumage, for instance, according to the locality from which they were obtained, it becomes possible to make the following general deductions:—

1. That the general uniformity is very much more marked than might have been expected considering the character for variability which has always been attributed to the bird; the variability is lost in the mass, though it is visible in individuals.
2. That, allowing for a good many exceptions, there is certainly a greater tendency to blackness in the birds of the northern Highlands than in those of the south.

Or, one may say that in passing from the north of

Scotland southward and westward there is an increasing tendency to the bright red and dark red types of Grouse, which culminate in the very characteristically bright red bird of Wales and of the Midlands of England, in which the predominating colour of the feathers of the breast and underparts generally is red with fine broken black cross-lines, and these are sometimes almost absent.

3. This gradual change from north to south of black, or red-and-black to dark-red cocks, and farther south to bright red cocks, is accompanied (speaking very broadly, for there are many exceptions) by a loss of the white terminal borders which characterize the feathers of the abdomen.

There is no doubt that the blacker birds of the Highlands in the north of Scotland are more frequently white-spotted beneath than the birds obtained farther south.

Nevertheless the white spotting is not confined to the blacker or to the darker birds, for it may be quite a conspicuous feature in the bright red birds of Wales and England, though in the lowlands and in the north of England, especially in Yorkshire, it is a rare character, only exceptionally met with.

Mr. Ogilvie-Grant, in his 'Handbook to the Game Birds,' 1896, says, "The ordinary varieties of the *male* may be divided into three distinct types of plumage: a *red form*, a *black form*, and a *white-spotted form*."

The *red form*, he says, "is mostly to be found on the low grounds of Ireland, the west coast of Scotland, and the Outer Hebrides"; and this statement is borne out not only by the Inquiry's collection of Grouse-skins, but by the interesting collection, made by Mr. T. E. Buckley, now in the Cambridge Museum. Similar birds have been obtained in some numbers from the following areas:—Caithness, Sutherland, the Lewes, and Inverness-shire. From Stirling, Selkirk, Northumberland, and Wicklow only one or two have been examined, but in Wales the red type is almost always met with. Welsh birds are often most typically and uniformly very bright red. Dumfriesshire also undoubtedly produces a large proportion of the same red type.

Bright red birds are not commonly characteristic of Ross-shire, Stirlingshire, or Northumberland, notwithstanding the fact that an occasional example of this type may be found there. Dumbartonshire, however, is said to produce more birds of a bright red type than any other, so also is Argyllshire, and both these counties fall in with Sutherlandshire as forming part of the west coast of Scotland.

The following specimens have been figured to illustrate the red form of the cock Grouse:—

Plate LXXXII. Upper surface, red type in winter-plumage.  
Male Grouse, No. 630. Wales, 18.iii.07.

Plate LXXX. Under surface, red type in winter-plumage.  
Male Grouse, No. 407. Glendoe, Inverness-shire,  
7.xii.06.

Plate LXXXIV. Under surface, red type, changing from winter- to autumn-plumage.

Male Grouse, No. 915. Forfarshire, 4.vi.07.

Plate XCVII. Under surface, variety of red type in autumn-plumage.

Male Grouse. Loch Sween, 19.viii.92. C. C. S. Parsons. Brit. Museum (Nat. Hist.), 92.7.13.1.

The second or *black form of cock* Grouse is, according to Mr. Ogilvie-Grant, rarely met with, most of the black birds being mixed with the red, or the white-spotted forms.

In the Committee's Collection there are a few very good examples of the really black type, and they come from the following areas:—Caithness, Sutherland, Perthshire, Dumbartonshire, and Yorkshire.

More or less typical examples have also been obtained from Ross-shire, Aberdeenshire, Morayshire, Kincardine, Stirling, Fifeshire, and Lancashire.

At Newcastleton, the low-lying grassy moors are credited with the production of the black type of Grouse, while the other types are found on the higher heather-ground.

The following specimen has been figured to illustrate the black type of cock Grouse:—

Plate LXXIX. Under surface: black type in winter-plumage.

Male Grouse, No. 723. Perthshire, 4.iv.07.

“The third or *white-spotted form* has the feathers of the breast and belly, and sometimes those of the head and upperparts, tipped with white. The most typical examples of this variety are found, as a rule, on the high grounds of the north of Scotland.”

This statement is again confirmed by the Grouse Inquiry's Collection, although an occasional white-spotted bird makes its appearance farther to the south. It is, however, the exception in the south, whether it be of the red or black or intermediate type.

The most marked examples of this white-spotted form have come from Caithness, Sutherland, and Inverness, while Dumfries, Perthshire, and Yorkshire have each provided one or two very fair examples.

At Dingwall birds are said to be most commonly dark red or black with white beneath.

At Scafton, Middleham, the majority have white beneath, and all are dark red or bright red.

The predominance of white beneath is quite conspicuous in a geographical arrangement of a large number of skins, as a character of the north of Scotland, especially throughout the Highlands.

The following specimen has been figured, illustrating the white-spotted type of cock Grouse:—

Plate LXXXI. Under surface: white-spotted form.

Male Grouse, No. 1377. Morayshire, 24.iv.08.

Turning next to the *female* Red Grouse, no less than five distinct types are described by Mr. Ogilvie-Grant:—

1. The red.
2. The black.
3. The white-spotted.
4. The buff-spotted.
5. The buff-barred.

The difficulty in sorting out hen Grouse into these classes is that a single bird may fall under three headings at once. A hen Grouse may be at once Buff-spotted, White-spotted, and Red or Black, for the white spotting is an independent character and may occur on any type in the autumn-plumage of the breast and abdomen, and this may also be definitely of the red or the black type.

In the Grouse Inquiry's Collection, the first or red type is well represented from all parts of the country, and follows very much the same distribution as the red type of the cock Grouse.

Red examples were procured from the following areas:—Sutherland (3), Argyll (9), Arran (1), Dumbarton (1), Cumberland (1), Westmorland (1), and Wales (3), all bright red birds; Ross-shire, all dark red; Inverness-shire, (3) very bright red and (3) very dark red birds; Aberdeen, (3) very dark red birds; Stirling, (4) red birds, with very fine black markings on the breast. Perthshire, Moray, Kincardine, Dumfriesshire, Kirkcudbright, Northumberland, Durham, and Yorkshire were all represented by red hens, generally of the dark red type.

The following specimen has been figured, illustrating the red type of hen Grouse:—

Plate LXXXVII. Under surface: red type changing from winter- to summer-plumage.

Female Grouse, No. 226. Roxburghshire, 22.v.06.

The second or black type of hen is certainly, as Mr. Ogilvie-Grant says, extremely uncommon, and only one or perhaps two of the Committee's birds should be included under this heading. Two others are, however, so dark as to come with difficulty under the category of red birds.

Caithness produced a really black hen bird (No. 418), the sex of which could not possibly have been determined from its plumage. It appears to be an old hen, which has assumed male plumage.

Specimen No. 338 from Inverness is almost as dark a bird, and No. 559 is a very dark reddish-black bird.

No. 414 from Dumbartonshire is similarly a case in which there seems to be more black than dark red.

The following specimen has been figured to illustrate the black type of female Grouse:—

Plate LXXXV. Under surface: black type in autumn-plumage.

Female Grouse, No. 418. Caithness, 31.xii.06.



The third or white-spotted type is less rare, and occurs, according to Mr. Ogilvie-Grant, much as it occurs in the male.

In the Committee's Collection it is well represented by birds from Sutherland (No. 1336); Ross-shire, a bird of the red type (No. 176); and Inverness (No. 329).

It was less to be expected that examples both of the red type and of a darker type, bordering on the black, should have been met with in Yorkshire, Lancashire, and Westmorland. Single examples were also procured in Dumfriesshire and Kincardine.

There is a fine Irish example from Co. Mayo in the British Museum (Natural History), No. 99.12.1.1.

The fourth or buff-spotted type of hen Grouse, said to be "much the commonest and most usually met with, has the feathers of the upperparts spotted at the tip with whitish-buff." This type is generally distributed, and the Committee's Collection includes examples from Caithness, Sutherland, Ross, Perthshire, Ayrshire, Kincardine, Dumfries, Northumberland, Yorkshire, Westmorland, and Lancashire.

The fifth or buff-barred form, according to Mr. Ogilvie-Grant, "is met with in the south of Ireland, and resembles in winter (autumn-plumage) the ordinary female in breeding plumage, having the upperparts coarsely barred with buff and black. Very little is known of this last variety, owing to the difficulty in obtaining birds, except during the shooting season."

Unfortunately, the repeated endeavours of the Grouse Inquiry Committee to obtain specimens proved unsuccessful, and one hen only was obtained from Donegal. This bird (No. 1217) was a very typical example of the buff-barred type, and it certainly differed from anything procured either in Scotland, England, or Wales.

Plate XCVIII. Under surface: buff-barred form in autumn-plumage.

Female Grouse, No. 1217. Donegal, Ireland, 17.x.07.

The nearest approach to it was to be found in four hens from Selkirkshire and in hens from Inverness-shire, which were more accurately described as buff-barred than as buff-spotted.

Single examples from Lanark, Midlothian, Roxburgh, Haddington, and Northumberland might be referred to the buff-barred type, and the females from Yorkshire were all rather of the buff-barred type, but none of these birds had quite the same markings as the Irish example. See Plate LXXXVI., Female Grouse, in full summer-plumage, Scottish buff-barred type.

Plates XCVII., XCIX., and CI. represent abnormal varieties of the Red Grouse and are drawn from specimens in the British Museum (Natural History). They are described on p. 1033 in the explanation of the Plates.

Two points in connection with the practical distinction of old Grouse from young, and of cock Grouse from hens, are of perennial interest both to the gamekeeper and to the sportsman.

No discussion is more apt to produce different opinions than that which arises upon the age or the sex of certain stages of moulting Grouse either at the luncheon hour upon the moor or in the game-larder when the day's bag has been overhauled, sorted out, and hung upon the hooks. It must be at once admitted that there are individual cases, by no means very rare, in which it is almost impossible to tell the sex with certainty until the bird has been cut open and the internal anatomy examined. In these doubtful cases the only way to settle the point is to cut the bird open down the middle of the abdomen, carefully turn over the whole of the intestines from the right to the left—that is, from the bird's left side to the bird's right side,—without tearing the attachments, and then, having exposed to view the flattened reddish portions of the kidney which lie closely packed on each side into the inequalities of the backbone and pelvis, to see whether the uppermost portion has overlying it an ovary or a testis.

In the breeding-season, and in a breeding bird, there can be no doubt whatever as to the sex, for the ovary is a conspicuous bunch of more or less developed ova in the hen; and in the cock the testis is a conspicuous round white object as large as the kernel of a good-sized hazel-nut on each side of the backbone.

There is but one ovary, and it lies always on the left side of the backbone of the bird. There are two testes, one lying on each side of the backbone, the left one generally at a slightly lower level than the right.

This development of the ovary only on one, the left, side is the reason for advising the examination to be made as described above, on the left side always. One testis or the ovary cannot then be missed.

If the bird examined thus is not breeding, as may often be the case with birds found dead of disease in April and in May, the discovery of the ovary is still a matter of comparative ease, and the discovery of the testes even easier. The testes are always somewhat enlarged in the spring months, whether the bird be diseased or not, and they may be the size of a pea or larger, and will generally be white. The ovary may be small, but will always be like a portion of hard cod's roe, in which the ova, though no bigger than a pin's head, are distinct and numerous. The undeveloped ovary of an adult female Grouse would about cover a threepenny piece, but is always rather long and triangular in shape instead of circular.

The oviduct in a breeding hen is a large and conspicuous part, and may, of course, contain an egg with the shell in course of formation, being pigmented in preparation for laying. The oviduct in a barren bird or in a hen not in the breeding-season is a very much less conspicuous object, and will be less easily found than the small and undeveloped ovary.

If no ovary is seen on examination, and a very small blackish, or whitish, or parti-coloured object is found in its place which is

suspected of being a testis, the intestines must then be gently separated from their attachments about the middle line of the back, and the other testis must be sought for in about the same position on the opposite side.

Even in a young bird the ovary shows ova with sufficient distinctness to make doubt as to its sex an impossibility; but in a very young male bird the testes may be so small, and, being very often quite black, may look so unlike what is expected that both should be sought for and found before arriving at a certain conclusion as to sex.

It is easy, if the intestines are roughly handled and the attachments torn carelessly away, to carry away the testes or the ovary from their proper position and to remove them with the intestinal attachments. The peritoneal folds are delicate and require careful handling, and they overlie the generative organs and the kidneys; but a very little practice will enable anyone to do the necessary dissection with certainty and to arrive at an irrefutable diagnosis as to sex.

It may be said that there is no other infallible means of arriving at the sex of a Grouse at certain times of the year, for it has so often happened that experienced and careful gamekeepers, who have handled Grouse for a lifetime, have sent in a paper filled in for a certain specimen as a cock, when the specimen has turned out to be a hen, and *vice versa*. The mistake is unavoidable and excusable, for in certain individual Grouse in the autumn-winter plumage there is no reliable characteristic in the feathering or in the supraorbital comb (Pl. XCV. figs. 1 & 2), or in any external part of the bird, by which the sex can be distinguished. In most Red Grouse, even in the vast majority, the confusion of sex is not possible, for it is a matter of common knowledge that for a great part of the year the cock and the hen are so wholly unlike one another as to make it difficult for anyone who did not know the birds to believe them to be of the same species. Even in the summer months, when the cock puts on a plumage closely simulating the breeding-plumage of the hen, there is a difference in the general tone and colour, and confusion is not likely. In the autumn and winter it is comparatively easy to mistake the sex of some individuals, when the hen has put on her autumn-plumage for the winter and the cock has put on his winter-plumage; certain individuals of opposite sex are then indistinguishable, even to the practised eyes of the experienced gamekeeper.

Generally speaking, the feathers of the head and neck give the best indication as to sex in the autumn-winter plumage. In the male the red colouring is, as a rule, far more uniform than in the female. In the male there is, as a rule, an absence of black markings on these red feathers, except on the upper part of the head, on the crown, and nape of the neck. The cheeks are generally a clear bronze- or chestnut-red colour; so are the feathers of the chin, throat, foreneck, and upper breast, giving

the bird a very rich uniform red colour all over the head and neck. In the hen, as a rule, the whole of the feathers of these parts are crossed by narrow black bars, which give her more of the mottled and broken colouring, which the cock bird begins to assume in the early summer when he puts on the first feathers of his autumn-plumage.

The feathers of the chin are a very useful indication of sex from August to November, practically throughout the shooting season, for the chestnut-red feathers which can be found on the chin of the cock Grouse in every month of the year will be sought for in vain in the hen from August to November. Even in December and January they are so imperfectly red as compared with the same red feathers in the male that one may almost say that red feathers are to be found on the chin of the hen only from February to July, when they become conspicuous on account of the contrast in colour with the increasing yellowness of the breeding-plumage of the hen. These red feathers persist in the hen exactly as do the feathers of the lower breast and abdomen, from her previous autumn-winter plumage.

This persistence of winter-plumage feathers on the chin, lower breast, and abdomen is common to both cock and hen; but in the cock they remain, as a rule, until replaced by the following winter-plumage, persisting throughout the autumn-plumage change; whereas in the hen they are persistent only to June or July, and are entirely replaced during the autumn-change.

Even when the autumn-plumage is put on, the yellow feathers of the preceding breeding-plumage are almost always to some extent persistent, and they are to be found in the chin of the hen bird even though the throat and neck may be unusually red and therefore unusually like those of a cock bird.

From January to May there is no possibility, as a rule, of confusing the sexes. In June and July it is unlikely, but in August and onwards to December it is sometimes quite easy to mistake them, and the best guide is the persistence of feathers of the preceding plumage such as occurs upon the chin in particular, recollecting that the dominating plumage of the male is the winter-plumage, while that of the female is the summer- or breeding-plumage.

In the autumn, especially from September and October onwards, there is the additional difficulty of distinguishing old birds and young.

"Young birds in July resemble the adult female in breeding-plumage in their general colour, but the flank-feathers of the adult plumage begin to appear about this time. By the month of November the young are generally not to be distinguished from the adults." This quotation is from Mr. Ogilvie-Grant's account.

There is one sign of age in the majority of birds in the shooting season, if it has not become obliterated—namely, the mark of recent shedding across the claws. Very often one may find the nails or claws still adhering to the toes, though ready to drop off, so that

a gentle application of force removes them like small caps, leaving the new shorter claws beneath, each marked by a groove where the old claw was attached. This groove persists often for some little time, and is as infallible a sign that the bird is at least a year old, as the presence of the claw itself ready to drop off. Young birds of the year do not shed their claws and therefore never have the groove.

There is another method of determining a bird's age which is often used as a rough indication upon the moor, namely, to pull out the third primary-feather of the wing at its distal end. If blood can be squeezed from the quill it is considered as a sign that the bird is of the year. If no blood can be squeezed and the feather is old and dry, it is considered as a sign that the bird is more than a year old.

This reasoning is based upon the following facts:—When a chicken produces its first set of primary wing-feathers they are all very thin and weak, and soon become frayed out; they have rather narrow pointed ends, and are blackish-brown, mottled with incomplete buff bars. Nine of these little feathers can be counted in series, and the weakest of all is the ninth counting from the distal to the proximal end. The growing power, as judged by the size of the root-sheaths of these feathers, increases from the ninth distally, so that at one period of growth (F) the feather No. 4 is the longest, then a little later (G) No. 3, then still later (H) No. 2. But No. 1 remains permanently shorter than No. 2.

By the time Nos. 1 and 2 are approaching full growth, the weak chicken-feathers Nos. 9, 8, 7, and so on have been shed, and in their place have appeared strong feather-roots growing strong round-ended uniform black primaries, instead of the weak, mottled, more narrowly pointed chicken-primaries.

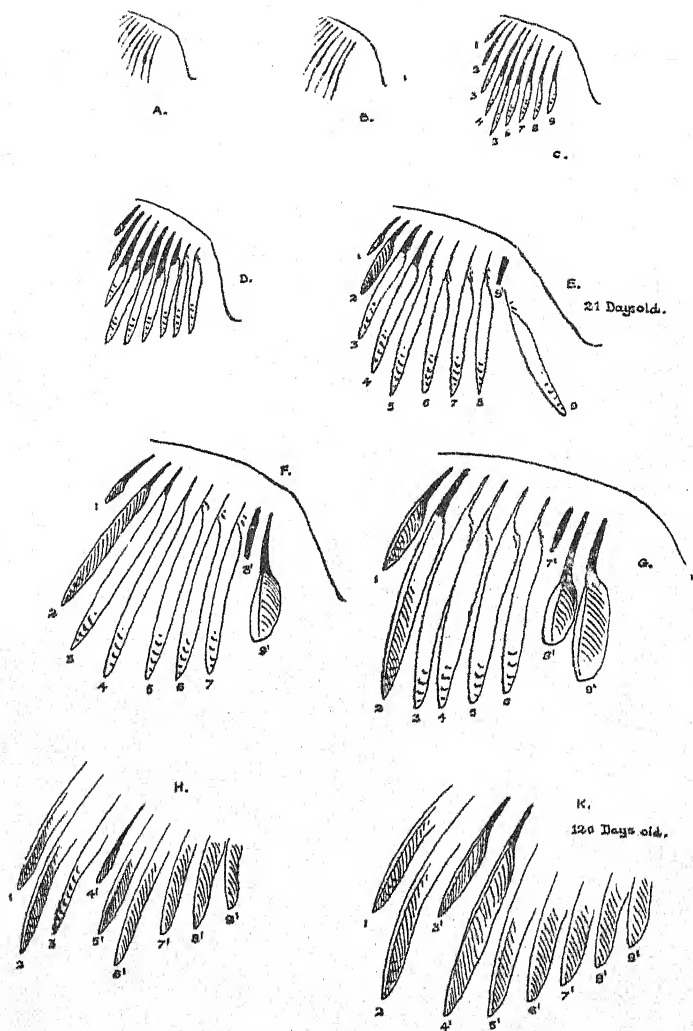
This shedding and replacement continues as far as No. 3 of the chicken-primaries, but when No. 3 falls out Nos. 2 and 1 are found to have grown into such long and strong feathers as to fall into the series of new replacement feathers, and so they remain, now fully grown, but can be recognised (K) by their more pointed ends having rather more of the buff markings on them than have the remainder of the primaries just grown from No. 9' to No. 3'. No. 3', moreover, being the latest of the whole series of primaries to have emerged, is for a time the shortest one; and, even when as long as No. 2, will be still the last one grown and will therefore upon withdrawal produce blood at the quill end when squeezed between the thumb and the finger.

The following diagrams (text-fig. 150) show very roughly this sequence of growth in the primaries of chick and pullet.

This sign of blood in the quill of the third primary is not an infallible sign of youth, for it is evident that as soon as the feather finishes its growth the quill becomes as hard and dry and bloodless as all the others. The only indication will then be a slight difference in the shape and contour of the last two feathers as indicated above.

Moreover, in September it is easy to find birds obviously adult with claws attached, but on the point of being shed, and having all the primaries moulted except the two most distal ones. The

Text-fig. 150.



Diagrammatic representation of the growth of Primaries in the young Grouse.

third then will be found to be a short feather actively growing and if it is pulled out the growing root will be full of blood.

Therefore not every bird that gives this sign is necessarily a bird of the year.

The condition of the ends of the primaries will, however, be a fair indication of age, and especially of the two most distal feathers.

Another sign often used to test the age of a bird is the strength of the lower jaw. The weight of the bird is allowed to hang without support by holding the tip of the lower bill only. The bone of an old bird's jaw easily stands this test, but the soft jaw of a young bird of three or four months cannot carry its weight, and the jaw either bends or breaks.

Yet another test is often tried by trying to crush in the skull with the thumb and finger: in the young bird the soft skull gives way readily, in the old bird it requires very considerable force.

In judging at a moment's notice whether a young Grouse chick which rises to the dogs on the 12th is of a shootable age and growth or not, the usual rule is probably as good a one as can be found—namely, that there should be a very clear view of black tail-feathers before the young bird is fit to kill.

It is only necessary, however, to look at a few young Grouse chicks of various ages to be convinced that more than a little of the black rectrices should appear before the bird is shot. Probably most sportsmen will be guided better by the strength of the bird upon the wing than by the black tail-feathers, however clearly visible in a half-grown chick.

In dissection, the age of an old bird is apparent, perhaps, as plainly upon the table as elsewhere. The fibrous tissues all toughen with age and use, and the bones become harder.

The grits of the gizzard in an old bird seem to be larger and more worn into rounded pebble shapes, and the reason for this has been fully discussed elsewhere.

The question, therefore, as to whether a bird is less than a year or more than a year old, may be answered, but it seems almost impossible to judge more exactly the age of a bird by any sign to be discovered either externally or internally.

#### EXPLANATION OF PLATES LXXVIII.—CI.

PL. LXXVIII. Pair of Red Grouse in summer with young chicks.

„ LXXIX. Male grouse in full winter-plumage; black type, underside. No. 723. Perthshire, 4.iv.07.

„ LXXX. Male grouse, in full winter-plumage; red type, underside. No. 407. Glendoe, Inverness-shire, 7.xii.06.

„ LXXXI. Male grouse, white-spotted bird of the red type; underside. No. 1377. Morayshire, 24.iv.08. 17½ oz.

„ LXXXII. Male grouse, in full winter-plumage, red type carrying a few black-centered feathers of the previous autumn-plumage; upperside. No. 630. Wales, 18.iii.07.

„ LXXXIII. Male grouse, showing very markedly the beginning of the autumn-plumage upon the head and neck; upperside. No. 1481. Inverness-shire, 8.v.08. 20 ozs.

- PL. LXXXIV. Male grouse, changing from winter- to autumn-plumage; red type, underside. No. 915. Forfarshire, 4.vi.07.
- „ LXXXV. Female grouse, in autumn-plumage, black type; underside. No. 418. Caithness, 31.xii.06. 21½ ozs.
- „ LXXXVI. Female grouse, in full breeding-plumage, Scottish buff-barred type; upperside. No. 226. Roxburghshire, 22.v.06. 20½ ozs.
- „ LXXXVII. Female grouse, changing from winter- to summer-plumage, red type; underside. No. 226. Roxburghshire, 22.v.06.
- „ LXXXVIII. Female grouse in full summer-plumage, underside. No. 217. Lanarkshire, 12.v.06.
- „ LXXXIX. Female grouse showing the bare broody patch of skin on the abdomen, and the beginning of a new growth of buff, broad-barred feathers in a double line down the abdomen; underside. No. 996. Argyllshire, 14.vii.07. 16 ozs.
- „ XC. Female grouse, red type, feathers from flanks. Natural size.  
Figs. *a* & *c* (from No. 1864), *g* & *h* (from No. 226), & *k* (from No. 632), are varieties of the spring flank-feathers.  
Fig. *b* (from No. 575) is a flank-feather from a very black hen.  
Fig. *d* (from No. 1864) is an example of what is termed fine-barred, dark-red winter-plumage, with narrow black bars or lines on rather dark rufous chestnut, the latter being slightly bleached towards the tip.  
Figs. *e* & *f* (from No. 1864) and *l* & *m* (from No. 664) illustrate intermediate stages of coloration, the feathers probably having broken through the skin when winter-conditions prevailed, and having completed their growth under summer-conditions.  
Figs. *i* & *n* (from No. 664) illustrate the reasoning upon which is based the view just mentioned; of these two feathers there is no doubt that *n* was being grown much later than *i*, and therefore more in summer-conditions, producing summer breeding-plumage.
- „ XCI. Female grouse, red type, upper tail-coverts showing effect of wear; the breakage has occurred in each case at the parts which are unpigmented or show the smallest amount of dark pigment. About 1½ times natural size.
- „ XCII. Grouse, red type, feet showing winter-plumage.  
Fig. 1. Right foot showing new winter-feathers and new nails (No. 1177).  
„ 2. Left foot showing full-feathered winter-plumage.
- „ XCIII. Feet of grouse, showing replacement of nails.  
Fig. 1. Right foot (No. 1148) with old nails ready to be shed.  
„ 2. „ „ in median vertical section.  
„ 3. Left „ (No. 1167). 3 *a*, old nails; 3 *b*, new nails; 3 *c*, shed nails.  
„ 4. Right „ (No. 1185) with new feathers and new nails.
- „ XCIV. Heads of Grouse.  
Fig. 1. Female. No. 61, 22.i.06. Showing the black markings on the throat.  
„ 2. Male. No. 545, 17.i.06. Showing the uniform chestnut throat.
- „ XCV. Supraorbital comb in Grouse and Ptarmigan.  
Fig. 1. Female Grouse (No. 1269, 8.ii.08.).  
„ 2. Male „ (No. 1268, 8.ii.08.).  
„ 3. Male Ptarmigan.
- „ XCVI. Supraorbital comb in Black-cock.
- „ XCVII. Scottish male grouse, showing abnormal erythrisms; underside. Loch Sween, Argyllshire. No. 19. 19.viii.92. British Museum (Nat. Hist.).
- „ XCVIII. Female grouse of the Irish buff-barred type; underside. Donegal, Ireland. No. 1217. 17.x.07. 22 ozs.
- „ XCIX. Female grouse, abnormal yellow variety; underside. Stornoway, Lewis, Hebrides, 30.x.1900. British Museum (Nat. Hist.).
- „ C. Female grouse, grey variety; underside. Perthshire, 6.x.89. British Museum (Nat. Hist.).
- „ CI. Female grouse, grey variety; underside. Type of *L. persicus* G. R. Gray, but probably from Perthshire. British Museum (Nat. Hist.).





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ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

April 5th, 1910.

Prof. E. A. MINCHIN, M.A., Vice-President, in the Chair.

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The Minutes of the last Scientific Meeting were confirmed.

The SECRETARY exhibited a series of photographs taken in the South Orkneys in 1908 by a correspondent of 'The Times,' and kindly sent him by the Editor of 'The Times.' The photographs included views of scenery and an interesting series of studies of living Seals, such as the Sea-Leopard (*Stenorhynchus leptonycus*), Weddell's Seal (*Leptonychotes weddelli*), the White, or Crab-eating Seal (*Lobodon circinophagus*), and Ross's Seal (*Ommatophaga rossi*).

Mr. R. I. Pocock, F.L.S., F.Z.S., exhibited a living specimen of a Mole-Rat (*Georychus*) recently presented to the Society by Capt. C. H. Armitage, who brought it from Ashanti. Mr. Pocock remarked that the animal possibly belonged to the species from Togoland described by Matschie as *G. zechi*, and certainly represented a form never previously exhibited in the Gardens.

Mr. R. H. WHITEHOUSE, M.Sc., introduced by the SECRETARY, gave an account of his Memoir on "The Caudal Fin of the Teleostomi." The paper dealt with the structure of the caudal fin in about fifty different species of fishes, mostly Teleostei, and representative of nearly all the sub-groups. After each sub-group a few general remarks were added, and these were followed by a short summary of results dealing with definitions and the taxonomic value of the caudal fin.

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\* This Abstract is published by the Society at 3 Hanover Square, London, W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Mr. T. M. S. ENGLISH read a paper, communicated by Mr. G. A. BOULENGER, F.R.S., V.P.Z.S., entitled "Some Notes on Tasmanian Frogs," based on observations made during rather more than two years' residence in Tasmania.

The paper by Mr. F. E. BEDDARD, M.A., F.R.S., "On the Alimentary Tract of certain Birds, and on the Mesenteric Relations of the Intestinal Loops," announced for this evening, was postponed owing to the indisposition of the Author.

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The next Meeting of the Society for Scientific Business will be held on Tuesday, the 19th April, 1910, at half-past Eight o'clock P.M., when the following communications will be made:—

1. STANLEY KEMP, B.A.

Notes on the Photophores of Decapod Crustacea.

2. J. LEWIS BONHOTE, M.A., F.L.S., F.Z.S.

On the Varieties of *Mus rattus* in Egypt, with General Notes on the Species having reference to Variation and Heredity.

3. G. E. BULLEN.

On an Example of Posterior Dichotomy in an Aylesbury Duckling.

---

The following communications have been received:—

1. F. E. BEDDARD, M.A., F.R.S.

On the Alimentary Tract of certain Birds, and on the Mesenteric Relations of the Intestinal Loops.

2. Prof. G. O. SARS, C.M.Z.S.

Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunningham, F.Z.S., 1904-1905. Report on the Ostracoda.

3. Dr. R. BROOM, D.Sc., C.M.Z.S.

On *Tritylodon*, and on the Relationships of the Multituberculata.

4. D. G. LILLIE, B.A.

Observations on the Anatomy and General Biology of some Members of the larger Cetacea.

H. B. FANTHAM, D.Sc., F.Z.S.

(5) The Morphology and Life-History of *Eimeria* (*Coccidium*) *avianum*: a Sporozoön causing a fatal disease among young Grouse.

(6) Observations on the Parasitic Protozoa of the Red Grouse (*Lagopus scoticus*).

(7) Experimental Studies on Avian Coccidiosis, especially in relation to young Grouse, Fowls, and Pigeons.

(8) Observations on the Blood of Grouse.

Communications intended for the Scientific Meetings of the ZOOLOGICAL SOCIETY OF LONDON should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

3 HANOVER SQUARE, LONDON, W.

*April 12th, 1910.*



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

April 19th, 1910.

Dr. S. P. HARMER, M.A., F.R.S. Vice-President, in the Chair.

The Minutes of the last Scientific Meeting were confirmed.

The SECRETARY read a Report on the additions that had been made to the Society's Menagerie during the month of March 1910.

On behalf of Mr. OLDFIELD THOMAS, F.R.S., F.Z.S., two specimens of the following new Monkey from the Malay Peninsula were exhibited :—

*PRESBYTTIS ROBINSONI*, sp. n.

Upper surface wholly white, scarcely relieved by a slight admixture of darker hairs. Underside, hands, and feet darker, greyish or greyish brown, varying in tone, but always darker than the crown and back.

*Hab.* Trung, Malay Peninsula.

*Type.* Adult male in British Museum. Original number 3184. Collected by H. C. Robinson, Esq., and presented by the Government of the Federated Malay States.

On behalf of Mr. OLDFIELD THOMAS, F.R.S., F.Z.S., a further consignment of small mammals from China, collected by Mr. Malcolm Anderson for the Duke of Bedford's exploration of Eastern Asia, was exhibited, and attention drawn to their value for the furtherance of zoological and geographical science.

The following forms were described as new :—

*MYOTIS MYOSOTIS ANCILLA*, subsp. n.

Smaller and with shorter ears than true *myosotis*. General colour drab. Forearm of type 61 mm.

*Hab.* Shang-chow, S.E. Shen-si. *Type.* Male. Original number 2082.

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*MICROTUS NUX*, sp. n.

Allied to *M. inez*, but darker and with a longer tail; 2nd and 3rd spaces of m<sup>3</sup> united.

Head and body 93 mm.; tail 39; hind foot 16.5.

*Hab.* Shang-chow, S.E. Shen-si. *Type.* Male. Original number 2089.

*MICROTUS JOHANNES*, sp. n.

Allied to *M. manularius*, but with smaller skull. Colour wood-brown instead of drab.

Head and body 95 mm.; tail 23; hind foot 17. Condylar-basal length of skull 24.6.

*Hab.* N.W. of Ko-lan-chow, Shan-si. *Type.* Male. B.M. No. 9.1.1.178.

Mr. J. LEWIS BONHOTE, M.A., F.L.S., F.Z.S., exhibited a yellow variety of *Mus rattus*. This individual had been bred from two wild-caught examples of *Mus rattus tectorum* from Egypt. The long hairs on the upper parts, which are normally black, were colourless and the shorter body-hairs had grey bases with yellow tips. As far as he knew, this was the first recorded example of a yellow rat, which was a colour quite unknown to fanciers and was never met with by Crampe or Doncaster, who had conducted colour-breeding experiments on Rats. Although it was not definitely stated, these experiments had probably been carried out with *Mus norvegicus*. A careful search through the large series of *Mus rattus* in the British Museum also failed to bring to light any yellow forms.

*Centenary of Philip Henry Gosse, F.R.S.*

*Born April 6, 1810; died Aug. 23, 1888.*

The SECRETARY exhibited the set of the works of Philip Henry Gosse in the Society's Library and gave a brief summary of his contributions to science, upon which he placed a very high value. The CHAIRMAN and Prof. A. SEDGWICK, F.R.S., added their testimony to his place in Zoological history; Dr. HENRY WOODWARD, F.R.S., gave some personal reminiscences; and Mr. EDMUND GOSSE, Librarian of the House of Lords, the son and biographer of Gosse, thanked the Society for their notice of his father's centenary.

Dr. W. T. CALMAN, F.Z.S., communicated a paper by Mr. STANLEY KEMP, B.A., entitled "Notes on the Photophores of Decapod Crustacean."

Mr. J. LEWIS BONHOTE, M.A., F.L.S., F.Z.S., read a paper on the variations of *Mus rattus*, founded on an examination of the forms of that species found in Egypt. The author pointed out that on examination of the hind-foot measurements of a considerable number he found that the curve showed three distinct apices, and that two of these apices belonged respectively to the

two forms found in Egypt, these forms being also more easily distinguished by their colour characteristics.

Mr. Bonhote in dealing with the Rats of this species from the Oriental Region had some years ago subdivided them into three subgroups, and it was now shown that the size of the feet typical of the three Oriental subgroups corresponded with the three apices in the curve of the Egyptian forms.

The author was inclined to think that these apices represented centres of variation and were probably inherited as Mendelian characters, for were this not the case the smallest apex would have become swamped and a regular curve would result.

It was, however, evident that the small foot character was present and ready to become the dominant form in a very short time should conditions giving advantage to a small foot arise.

On comparing the curve of the hind feet of *Mus norregicus*, three apices were also observed, showing that in this species the "hind foot character" was also present, but as there were no corresponding colour differences it was impossible to tell to which group any particular individual belonged.

The author drew the following conclusion, viz., that there was considerable *prima facie* evidence that the size of the hind foot and the colour of the hairs on the underparts were Mendelian characters, and pointed out that the former character was also found in another species, *Mus norregicus*, and the latter in a third species, *Mus musculus*.

On the presumption that these were true Mendelian characters a clearer understanding was at once gained as to how species might very quickly adapt themselves to altered conditions, and how many very closely allied species, differing only in size or in some definite but slight alteration of colour, could exist in the same locality and yet maintain their characteristics intact and show no merging of the one into the other.

Experiments in breeding the different forms were being undertaken, but they were not as yet sufficiently advanced to permit of any definite results being stated.

Mr. G. E. BULLEN presented a paper, communicated by Mr. JOHN HOPKINSON, F.Z.S., "On an Example of Posterior Dichotomy in an Aylesbury Duckling," giving a detailed account of a dissection performed on a duckling having supernumerary legs. In addition to a reduplicated pelvis and the usual condition of the limbs presented in posterior dichotomy, it was found that the specimen showed evidence of a further reduplication of the part dichotomised.

The next Meeting of the Society for Scientific Business will be held on Tuesday, the 3rd May, 1910, at half-past Eight o'clock P.M., when the following communications will be made :—

H. B. FANTHAM, D.Sc., F.Z.S.

(1) The Morphology and Life-History of *Eimeria (Coccidium) avium*: a Sporozoön causing a fatal disease among young Grouse.

(2) Observations on the Parasitic Protozoa of the Red Grouse (*Lagopus scoticus*).

(3) Experimental Studies on Avian Coccidiosis, especially in relation to young Grouse, Fowls, and Pigeons.

(4) Observations on the Blood of Grouse.

5. Prof. G. O. SARS, C.M.Z.S.

Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunningham, F.Z.S., 1904-1905.—Report on the Ostracoda.

6. Dr. R. BROOM, D.Sc., C.M.Z.S.

On *Tritylodon*, and on the Relationships of the Multituberculata.

The following communications have been received :—

1. F. E. BEDDARD, M.A., F.R.S.

On the Alimentary Tract of certain Birds, and on the Mesenteric Relations of the Intestinal Loops.

2. D. G. LILLIE, B.A.

Observations on the Anatomy and General Biology of some Members of the larger Cetacea.

3. C. F. ROUSSELET, F.R.M.S.

Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunningham, F.Z.S., 1904-1905.—Report on the Rotifera.

Communications intended for the Scientific Meetings of the ZOOLOGICAL SOCIETY OF LONDON should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

3 HANOVER SQUARE, LONDON, W.

April 26th, 1910.

ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

May 3rd, 1910.

Dr. A. SMITH WOODWARD, F.R.S., Vice-President, in the Chair.

The Minutes of the last Scientific Meeting were confirmed.

The SECRETARY exhibited a photograph of a Giraffe, kindly lent him by Mr. Carl Hagenbeck. The animal was an adult female 3.30 metres in height, obtained in Gallaland, East Africa, and was in the possession of Mr. Hagenbeck. It displayed a reticulate coloration, in which the lighter areas were reduced to narrow lines, clearly on the neck and body, but the hind-quarters were blotched, whilst the spotting came lower down on the legs than in the typical *Giraffa reticulata*. It possibly represented a type intermediate between *G. reticulata* and *G. camelopardalis*, but it was to be remembered that the specimen was a female, and that females did not exhibit the coloration so conspicuously as old males.

Mr. E. E. AUSTEN, F.Z.S., exhibited a specimen of a rare Fly (*Cephenomyia ulrichii* Brauer) from East Prussia, parasitic in the larval stage in the throat of the Elk (*Alces machlis* Ogilby), and remarked on its habits and those of allied species. This specimen had been recently acquired by the Hon. Charles Rothschild and presented by him to the British Museum.

Dr. R. A. O'BRIEN, introduced by Prof. E. A. MINCHIN, M.A., F.Z.S., exhibited a series of lantern-slides illustrating the habits of the North Queensland Green Tree-Ant (*Oecophylla smaragdina*?), and described the method of nest-building and bridge-forming followed by these insects.

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\* This Abstract is published by the Society at 3 Hanover Square, London, W., on the Tuesday following the date of Meeting to which it refers. It will be issued, along with the 'Proceedings,' free of extra charge, to all Fellows who subscribe to the Publications; but it may be obtained on the day of publication at the price of *Sixpence*, or, if desired, sent post-free for the sum of *Six Shillings* per annum, payable in advance.

Dr. H. B. FANTHAM, F.Z.S., exhibited, on behalf of Miss A. PORTER, B.Sc., and himself, preparations and original drawings of a new *Trypanoplasma* (*Cryptobia*) from the alimentary tract of *Dendrocoelum lacteum*. The parasites measure from  $20\mu$  to  $40\mu$  long approximately. They are biflagellate, the posterior flagellum forming the border of an undulating membrane. The blepharoplast (kinetonucleus) is large and curved. It is proposed to call the parasite *Trypanoplasma* (*Cryptobia*) *dendrocali*. There is evidence of hereditary infection of the Planarian by the *Trypanoplasma*, for the parasites have been seen to enter the eggs of the host. A Trypanosome-like flagellate was also seen on rare occasions in the guts of *Dendrocoelum lacteum* and *Planaria nigra*. It is interesting to record, for the first time so far as is known, the occurrence of a *Trypanoplasma* in a vegetable feeder like *Dendrocoelum*.

Dr. H. B. FANTHAM, F.Z.S., Protozoologist to the Grouse-Disease Inquiry, read four papers relating to the Protozoa and blood of Grouse, illustrated by lantern-slides made from the original plates accompanying the memoirs.

The first paper, entitled "The Morphology and Life-History of *Eimeria* (*Coccidium*) *avium*: a Sporozoön causing a fatal disease among young Grouse," gave a detailed account of the morphology and life-history of the Coccidium which destroys the epithelial lining of the duodenum and caeca of Grouse chicks, causing enteritis accompanied by diarrhoea.

The second paper, entitled "Observations on the Parasitic Protozoa of the Red Grouse (*Lagopus scoticus*)," set forth the author's observations on some seven other Protozoa, parasitic in the blood or in the digestive tract of Grouse. None of these parasites, however, could be said to be either numerous or very harmful to the birds examined. The parasites were *Leucocytozoön lovati*, in which schizogony in the spleen of the bird was recorded for the first time, not only for *Leucocytozoön lovati* but for any avian *Leucocytozoön*; *Hamoproteus mcnsoni* and *Spirochaeta lagopodis* in the blood; *Trichomonas eberthi* and *Spirochaeta lovati* in the caeca; and *Amoeba lagopodis* in the intestine and faeces. The Spirochaetes and Amoeba of Grouse are new species. *Monocystis* spores are also found occasionally. All the parasitic Protozoa mentioned were observed both alive and in stained preparations.

The third paper dealt with "Experimental Studies on Avian Coccidiosis, especially in relation to young Grouse, Fowls, and Pigeons." The results of many and varied experiments were recorded in this paper, relating to the time of ripening and duration of infectivity of coccidian oöcysts, their dispersal by insect larvæ &c., and the effects of various reagents on the oöcysts. The distribution of the parasites within the host was given and the results of the transmission of Grouse coccidiosis to young fowls and pigeons were set forth.

"Observations on the Blood of Grouse" were discussed by the author in the fourth and last paper. The various blood-cells were described, and the results of blood counts (both of red cells and of leucocytes differentially) of healthy and diseased birds were set forth. Both coccidiosis and strongylosis produce anaemia, and the presence of various parasites is also associated with numerical differences in the leucocytic elements of the blood.

Dr. W. A. CUNNINGTON, F.Z.S., communicated a paper by Prof. G. O. SARRS, C.M.Z.S., containing the Report on the Ostracoda collected by the Third Tanganyika Expedition during 1904-1905.

Dr. A. SMITH WOODWARD, F.R.S., communicated a paper by Dr. R. BROOM, D.Sc., C.M.Z.S., "On *Tritylodon*, and on the Relationships of the Multituberculata." The author had re-examined the type and only known specimen of *Tritylodon*, and in one or two points came to different conclusions from Owen and Seeley. The large flat piece of bone which forms the upper part of the snout, regarded by both Owen and Seeley as the frontal, was believed to be the upper part of the nasal. The supposed parietal was held to be the frontal. No distinct prefrontal could be made out; but there was believed to be a large distinct septomaxillary. The dental formula was believed to be  $i^3 m^7$ , instead of, as supposed by Owen,  $i^2 m^6$ .

Kidley's recent paper on *Ptilodus* was criticised at some length, and an endeavour made to controvert his conclusion that *Ptilodus* is allied to the Diprotodont Marsupials.

It was held that while the Multituberculates are doubtless very unlike the living degenerate Monotremes, they are more primitive than the Marsupials and not at all closely allied to them, and that till the evidence of their affinities is much greater than at present they may well be left as an independent order.

The next Meeting of the Society for Scientific Business will be held on Tuesday, the 24th May, 1910, at half-past Eight o'clock P.M., when the following communications will be made:—

1. D. G. LILLIE, B.A.

Observations on the Anatomy and General Biology of some Members of the larger Cetacea.

2. C. F. ROUSSELET, F.R.M.S.

Zoological Results of the Third Tanganyika Expedition, conducted by Dr. W. A. Cunningham, F.Z.S., 1904-1905.—Report on the Rotifera.

3. JAMES RITCHIE, M.A., B.Sc.

The Marine Fauna of the Mergui Archipelago, Lower Burma, collected by Jas. J. Simpson, M.A., B.Sc., and R. N. Rudmose-Brown, D.Sc., University of Aberdeen, February to May, 1907.—The Hydroids.

4. JAMES RITCHIE, M.A., B.Sc.

Hydroids from Christmas Island, Indian Ocean, collected by C. W. Andrews, D.Sc., F.R.S., F.Z.S., in 1908.

The following communications have been received:—

1. F. E. BEDDARD, M.A., F.R.S.

On the Alimentary Tract of certain Birds, and on the Mesenteric Relations of the Intestinal Loops.

2. R. I. Pocock, F.L.S., F.Z.S.

On the Cutaneous Scent-glands of Ruminants.

3. R. LYDEKKER.

On a Pair of Wapiti Antlers and a new Muntjac.

Communications intended for the Scientific Meetings of the ZOOLOGICAL SOCIETY OF LONDON should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

3 HANOVER SQUARE, LONDON, W.

May 10th, 1910.

ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

May 24th, 1910.

Dr. HENRY WOODWARD, F.R.S., Vice-President, in the Chair.

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The Minutes of the last Scientific Meeting were confirmed.

The SECRETARY read a Report on the additions that had been made to the Society's Menagerie during the month of April 1910.

Mr. ERNEST GIBSON, F.Z.S., exhibited a skin of *Felis geoffroyi* and made some remarks on the distribution of the animal.

Mr. D. G. LILLIE, B.A., read a paper, communicated by Dr. H. GADOW, F.R.S., F.Z.S., entitled "Observations on the Anatomy and General Biology of some Members of the larger Cetacea." This paper was the outcome of seven weeks spent at the Irish whaling station during the summer of 1909. The object of the visit was to make a preliminary survey of the opportunities which are now offered for a study of the larger Cetacea by the recent establishment of whaling stations off the shores of the British Isles. It was pointed out that hitherto our knowledge of whales had been chiefly derived from the examination of stranded specimens, which had often reached an advanced state of decay; whereas it was now possible to obtain a plentiful supply of large whales fairly near at hand which were sufficiently fresh for histological study. It was particularly desirable to increase our knowledge of the larger Cetacea before these much-hunted animals became too scarce. A list was given of the species captured at the Irish station during the two years of its existence, with notes on the species *Balaenoptera musculus* Linn., *B. sibbaldii* Gray, and *Physeter macrocephalus* Linn., which were seen by the author.

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The paper also contained observations on the occurrence of hairs in whales; the auditory organ of the *Balaenoptera*; the asymmetry of the odontocete skull; and a few remarks upon the habits of whales. In conclusion, attention was called to the present difficulty in obtaining information as to their method of copulation, period of gestation, rate of breeding, &c., and a means of overcoming this difficulty was suggested.

Mr. C. F. ROUSSELET, F.R.M.S., read a paper, communicated by Dr. W. A. CUNNINGTON, F.Z.S., on the collection of Rotifera made by the Third Tanganyika Expedition, 1904-1905. Amongst the specimens brought back by Dr. W. A. Cunningham were a number of tubes containing fine surface plankton nettings from Tanganyika and other lakes of that region. These the author searched for Rotifera, and the result was contained in the present paper. From Lake Tanganyika only 11 species were obtained, all already known in other parts of the world; whilst the River Lofu, which enters the lake at its south-western corner, yielded 23 species, one of which is a very remarkable new kind. In Lake Nyassa only 6 species were found, and a single gathering of Victoria Nyansa yielded 9 species. This collection is interesting and important from the fact that no previous record of Rotifera from Lake Tanganyika had been made, and very few species were known from the Central African Region.

A complete list of species of Rotifera so far known from this region was appended.

Mr. R. KIRKPATRICK, F.Z.S., communicated two papers by JAMES RITCHIE, M.A., B.Sc., of the Royal Scottish Museum, on the Hydroids of the Mergui Archipelago, collected by Mr. J. J. Simpson and Dr. R. N. Rudmose Brown; and on the Hydroids of Christmas Island, collected by Dr. C. W. Andrews, F.R.S. The chief interest of these two papers was faunistic. In the former 30 species were recorded, in the latter 13. It was apparent that the Hydroid fauna of the Eastern Indian Ocean, of which hitherto little had been known, lacked distinctness, and that its closest affinities were with the faunas of the neighbouring Malay Archipelago and Australian areas.

The next Meeting of the Society for Scientific Business (closing the Session 1909-1910) will be held on Tuesday, June 14th, 1910, at half-past Eight o'clock P.M., when the following communications will be made :—

1. R. I. Pocock, F.L.S., F.Z.S.

On the Cutaneous Scent-glands of Ruminants.

2. R. LYDEKKER.

On a Pair of Wapiti Antlers and a new Muntjac.

3. R. LYDEKKER.

On Three African Buffaloes.

4. A. CABRERA, C.M.Z.S.

On Two new Antelopes.

5. Dr. E. A. WILSON, F.Z.S.

The Plumage of the Grouse.

The following communication has been received :—

F. E. BEDDARD, M.A., F.R.S.

On the Alimentary Tract of certain Birds, and on the Mesenteric Relations of the Intestinal Loops.

Communications intended for the Scientific Meetings of the ZOOLOGICAL SOCIETY OF LONDON should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

3 HANOVER SQUARE, LONDON, W.

May 31st, 1910.



ABSTRACT OF THE PROCEEDINGS  
OF THE  
ZOOLOGICAL SOCIETY OF LONDON.\*

June 14th, 1910.

Dr. S. F. HARMER, M.A., F.R.S., Vice-President,  
in the Chair.

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The Minutes of the last Scientific Meeting were confirmed.

The SECRETARY read a Report on the additions that had been made to the Society's Menagerie during the month of May 1910.

Mr. R. I. Pocock, F.L.S., F.Z.S., exhibited drawings to illustrate an apparently unrecorded instance of ant-mimicry by the larvæ of a species of *Mantis* from Axim, on the Gold Coast.

Mr. R. I. Pocock, F.L.S., F.Z.S., read a paper "On the Cutaneous Scent-glands of Ruminants," based principally upon work done at the Prosectorium on animals that had died in the Gardens. The paper was illustrated by lantern-slides showing the macroscopic structure of the preorbital, pedal, and inguinal and other specialised glands of most of the genera of this group of Ungulates. The author pointed out that the structure of the feet, whether furnished with special glands or not, supplied valuable data for classifying the genera of Antelopes and Deer; and showed that with some modifications, such as the removal of *Tetracerus* from the Cephalophinae to the Tragelophinae, of *Dorcotragus* from the Antilopinae to the Neotraginae, and of *Pantholops*, *Saiga*, and *Pygoceros* from the Antilopinae, the sub-families usually admitted were valid groups. In the case of the Deer it was interesting to note that *Kucervus*, *Panolia*, *Elaphurus*,

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and *Sika* were closely allied to *Cervus*, *Dama* being a totally distinct type. *Axis* and *Hyalaphus* belonged to another group, while *Rangifer*, *Alces*, and *Capreolus*, as Sir Victor Brooke claimed, belonged to the section typified by *Dorcylaphus*, *Mazama*, and other American Deer.

Mr. R. LYDEKKER communicated a paper "On a Wapiti and a Muntjac," in which he described two Wapiti antlers from Tibet as *Cervus canadensis wardi*; and a Muntjac from An-wei, China, as *Cervulus bridgmani*. The latter was characterised by its dark blackish-olive colour, the black ears of the female and the yellow ones of the male, coupled with the relatively wide divergence of the antler-pedicles.

Mr. R. LYDEKKER also presented a paper "On Three African Buffaloes."

Dr. A. CARRERA, C.M.Z.S., communicated a paper "On Two new Antelopes," in which he described a new species of *Dama-liscus* from British East Africa and a new Chamois from North Spain.

Mr. W. R. OGILVIE-GRANT, F.Z.S., communicated a paper by Dr. E. A. WILSON, F.Z.S., Field Observer to the Grouse Disease Committee, entitled "Changes of Plumage in the Red Grouse (*Lagopus scoticus*) in Health and Disease."

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This Meeting closes the Session 1909-1910. The next Meeting of the Society for Scientific Business will be held on Tuesday, November 15th, 1910, at half-past Eight o'clock p.m.

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The following Papers have been received:—

1. F. E. BEDDARD, M.A., F.R.S., F.Z.S.

On the Alimentary Tract of certain Birds, and on the Mesenteric Relations of the Intestinal Loops.

2. E. H. J. SCHUSTER, F.Z.S.

Cortical-cell Lamination of the Hemispheres of *Papio hamadryas*.

3. Prof. ALEX. MEER, F.Z.S.

A Contribution to our Knowledge of the Development of the Brain and of the Nose of the Crocodile, *Crocodilus porosus*.

Communications intended for the Scientific Meetings of the  
ZOOLOGICAL SOCIETY OF LONDON should be addressed to

P. CHALMERS MITCHELL,

*Secretary.*

3 HANOVER SQUARE, LONDON, W.

June 21st, 1910.



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